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# Inheritance Studies in the Onion, *Allium Cepa* L.

Warid Abdel bar Warid

*Louisiana State University and Agricultural & Mechanical College*

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**INHERITANCE STUDIES IN THE ONION, ALLIUM CEPA L.**

**A Dissertation**

**Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy**

**in**

**The Department of Botany,  
Bacteriology, and Plant Pathology**

**by**

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B.S., Fouad 1st University, 1943  
M.S., Louisiana State University, 1949  
June, 1952**

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## ABSTRACT

An investigation concerning the inheritance of some economic characters in onion was undertaken. Data were obtained, in 1949 - 1952, from parent selections and from  $F_2$  and backcross progenies.

Four crosses made in 1948, between the Red Creole and Calred varieties of onion, provided the material for this study.

The mode of inheritance of resistance to downy mildew, inheritance of soluble solids, inheritance of pigments, inheritance of scape production (bolting), and inheritance of length of dormancy was discovered or confirmed. The magnitude of any one pair of allelomorphic characters, in parents, was very wide.

The mode of inheritance of male sterility in American-Egyptian hybrids of onions was revealed.

The biometrical constants, the "chi-square" method for testing goodness of fit, and the correlation coefficients were used for the study of the inheritance of most of the characters.

The resistance of scapes to downy mildew was inherited as a recessive character, determined by two duplicate recessive genes ( $s_1$  and  $s_2$ ) possessed by the resistant Calred parent. No association was found between the degree of foliage infection and that of scape infection.

The frequency polygon of percent soluble solids in the  $F_2$  was unimodal, indicating quantitative inheritance controlled by multiple genes. Four to ten pairs of genes may govern the percentage of soluble solids, and probably act in a geometric manner, with partial dominance of the low-solids percentage. A high degree of heritability in the percentage of soluble solids was demonstrated.

It was confirmed that albinism was inherited as a monogenic recessive character. No relationship was found between the incidence of albinism and percentage germination in a population of which some individuals carried the albino gene, a.

Dark-red color of onion bulbs was found to be dominant over light-red color, and there were two to four pairs of genes acting as modifiers for the red-color intensity.

The non-bolting character showed absence of dominance. Bulbs stored in cold storage (35° F.) showed a significantly lower percentage of bolters than those bulbs which were in common storage. The degree of foliage infection in the first growing season had no influence on the percentage of scapes produced in the second growing season.

The sprouting character of bulbs, after 17 or 20 weeks in storage, showed absence of dominance. Bulbs of bolted plants kept in storage as well as bulbs of non-bolted plants. Through backcrossing, using the Red Creole as the recurrent parent, some improvement of the storage quality was achieved by reducing the percentage of rots.



Giza 6, an Egyptian onion variety, was found to possess the male-sterile gene ms in a heterozygous condition. The male-sterile character of Italian Red 13-53 (determined by plasmagene S and the homozygous recessive chromogene ms), after being incorporated into the Excel, an American variety of onion, was successfully transferred to a line of Giza 6.

## INTRODUCTION

The onion is of Old World origin and has been used as a food plant from the earliest historic times. It was an important article of diet in Egypt at the time of the building of the pyramids, and Moses, in his account of the exodus of the Children of Israel from Egypt, mentioned it as one of the articles of food for which the Israelites longed during their sojourn in the wilderness (12).

Onion takes its name from the city built by Onias (B.C. 173) near the Gulf of Suez. It is now grown in all temperate regions of the world, especially in Egypt, Spain, Italy, and the United States. By 1390 this vegetable was extensively used in Europe and was brought to this country by the earliest Colonists. It is first mentioned as being cultivated in America in 1629 (39).

The annual onion crop in the United States (1939-1948) averaged 37,740,000 sacks (50-pound sack) and was grown on 131,580 acres. Acreage in 1949 was 120,960 and the production was 37,830,000 sacks (209).

The peak of the onion acreage in Louisiana was reached in 1927 when 2,900 acres were grown and the yield per acre was 108 sacks (50-pound sack). Since that time the acreage has fluctuated widely and a low point of 500 acres was reached in 1933 after poor yields obtained

in the preceding years. In 1949 the Louisiana acreage was 1,300 acres, and the yield was 100 sacks per acre (132). Epiphytotics of downy mildew which occurred over a period of several years were largely responsible for the low yield and the abandonment of onion growing.

Knowledge of the botanical description of the onion plant is important in relation to the various plant characters investigated. The common onion belongs to the genus *Allium* which was recently placed in the family Amaryllidaceae (*Amaryllis* family). The genus contains about 500 species in the northern hemisphere, many native in North America, with strong characteristic odor. A very few are grown for ornament and others as vegetable-garden subjects (9).

The common onion, *Allium Cepa* L., is potentially a biennial. The scape (seedstalk) is hollow, swollen below the middle, and much taller than the leaves. The inflorescence is a terminal umbel, and is subtended by a papery spathe consisting of 2 or 3 bracts which enclose the umbel until it is split by the development of the first flowers. The flowers are regular and of lilac or nearly white color, consisting of a perianth of 6 similar parts arranged in two whorls, 6 stamens inserted at the base of the perianth segments in two cycles, and a pistil of three undiverged carpels. The nectaries occur in the axils of the three inner stamens. The ovary is superior and there is a single, thin persistent style with a slightly three-lobed stigma. The anthers of the inner whorl of stamens dehisce before those of the other, and both sets do so before the stigma is receptive. For this reason, cross-fertilization is the rule and is effected through the agency of insects (9, 72).

The correct botanical term for what is commonly known as onion seedstalk (or seed-stem, or flower-stalk) is scape. The scape is defined by Bailey (9) as a leafless peduncle arising from the ground; it may bear scales or bracts but no foliage-leaves and may be one- or many-flowered.

The bulb consists of a short stem which bears a series of thickened leaves and leaf bases, together with the cycles of adventitious roots. The arrangement of the leaves is concentric so that the elder ones surround the younger, and the apical meristem is located at the center of the bulb.

In a full-sized mature bulb, some of the inner leaves do not develop an elongated blade, and the functional blades of the outermost six or seven leaves become dry and break off so that only the sheaths remain. These protect the fleshy storage leaves which surround 3 or 4 leaves with short undeveloped blades; and central to the latter are successively younger leaves with longer blades. After passing the dormancy period the bulb sprouts, that is, the youngest leaves continue development. The storage leaves outside them also elongate, especially at the base, but their green blades remain relatively small. As the inner leaves are growing, the outer storage leaves progressively dry up because of the withdrawal of food reserves and moisture (72).

## MATERIALS

In the spring of 1948, Dr. H. A. Jones made several crosses between the Galred and the Red Creole varieties of onion in his greenhouses at Beltsville, Md.

In the 1948-49 season,  $F_1$  plants of this cross were grown at Baton Rouge, La. Some of the  $F_1$  plants produced scapes at Beltsville, and Dr. Jones was able to self some of these plants and  $F_2$  seeds were obtained.

In the 1949-50 season, seeds of the parental varieties (not the specific parental plants),  $F_2$ , and bulbs of  $F_1$  were planted and tested in Baton Rouge. Some  $F_2$  seeds were planted in Greeley, Colorado early in 1950, and the bulbs produced were sent to Baton Rouge in August 1950. In Beltsville, the first backcrosses were made by the writer under the supervision of Dr. Jones and seeds were obtained.

In the 1950-51 season, the parental varieties (from seeds and bulbs),  $F_1$  (bulbs),  $F_2$  (from seeds and bulbs), and the first backcross (from seeds) were grown in Baton Rouge. In the spring of 1951, some  $F_2$  plants were selfed and  $F_3$  seeds were obtained.

In the 1951-52 season, the breeding material, including  $F_3$  lines, was grown in Baton Rouge, but no data on downy mildew was recorded.

### Crosses Tested

Four crosses and two first generation backcrosses were tested throughout the investigation. These were:

- I. Calred (plant #944) x Red Creole (plant #945)
- II. Calred (plant #946) x Red Creole (plant #945)
- III. Calred (plant #950) x Red Creole (plant #945)
- IV. Red Creole (plant #949) x Calred (plant #946)

Different Red Creole plants were used in the following two backcrosses:

- V.  $F_1$  (Red Creole #949 x Calred #946) x Red Creole
- VI.  $F_1$  (Red Creole #949 x Calred #946) x Red Creole

### Parents' Description

Red Creole: This variety has several synonyms, viz. Creole, Louisiana Creole, Louisiana Red Creole, and Pale Red Creole. It has been grown on Bayou Lafourche, La., for well over 100 years. The original variety from which it was developed is not known, although it is supposed to be of Italian origin. Local growers still maintain strains that have been in the family for generations and these strains differ slightly in type (121, 129).

Red Creole seems to be fairly well adapted to the southernmost districts of the Southeast and along the coast as far north as Charleston, S. C. At present it is of commercial importance only in southern Louisiana, where it is the chief variety for home and market purposes because it keeps better in open sheds or barns during the humid summer than any other variety. The bulbs are flat to

medium oblate in general shape. The bulb color is dull buff red, and the epidermis of outer fleshy scales is medium purplish red with succeeding scales lighter in color toward the center. The outer dry scales are retained fairly well in handling and storage. The bulbs have a high dry-matter content and are very pungent and firm in texture. The foliage and the scapes of the Red Greole are highly susceptible to downy mildew (98, 121).

Calred: This variety was developed and introduced cooperatively by the California Agricultural Experiment Station and the United States Department of Agriculture. It is adapted to the South and Southwest. It is highly nonbelting. The bulbs are deep flat and very dark red, with outer scales a little lighter in color. The flavor is mild (98).

Calred is a fertile selection from a cross of male-sterile Italian Red x Lord Howe Island. The developmental history of Calred is indicated by its pedigree (13-53 x 10) x 10) op 1 - cag 2 - op 1, which indicates that:

1. The original cross was 13-53 x Lord Howe Island. The strain 13-53 is a selection of Italian Red.
2. A selected bulb from this progeny was backcrossed to Lord Howe Island.
3. Selected bulbs from the backcross population were massed in an isolated plot.
4. Selected bulbs from the open-pollinated generation were massed under a cage.
5. Selected bulbs from seed produced in step 4 were again caged.
6. A final mass open pollination in isolation was made with bulbs grown from seed produced in step 5.

The scapes of Calred (released in 1947) are highly resistant to the race of downy mildew present in central California, with the foliage moderately resistant (27).

Italian Red 13-53: This strain of onion has historical importance. It is a selection from the variety Italian Red. The bulbs of this variety are torpedo-shaped, large, red, mild-flavored, and poor keepers.

The Italian Red population from which strain 13-53 was selected was grown in Davis, Calif. in 1924. In August, a considerable number of desirable bulbs were selected and planted for self-pollination. In April, 1925, the umbels were covered with manila-paper bags when the first flowers opened. These bagged heads were harvested on August 8. From the 5 seed heads of plant 53, 136 bulbils were secured, but no seed. This discovery appeared to have no immediate practical importance, but certainly was of value in a study of sterility and in the development of hybrid onions. By means of bulbils, 13-53 has been asexually propagated since 1925 (91, 96).

Lord Howe Island: The seed of this variety was secured from Australia. The bulbs are early maturing, deep red, oblate, and very mild-flavored. They do not keep well in storage (154).



## GENERAL EXPERIMENTAL METHODS

### Crossing Technique:

The umbels of the plants to be crossed are covered with 1-pound manila paper bags as soon as the first flower opens. At first only a few flowers of an umbel open daily; then the number mounts gradually until full bloom. Those on the plant that is to be used as the female parent must be removed several times each day. If the weather is hot, this must be done more often, because the anthers shed their pollen soon after the flowers open, thereby contaminating the umbel. It was found that a period of 23 hours had to elapse from the time of full expansion of the perianth, before all the anthers of any flower had dehisced (94). The pollen is usually shed between 9 a.m. and 5 p.m.

All the open flowers are thus removed until full bloom; then emasculation of the remaining flowers is begun. When 50 or more have been emasculated (anthers removed), the remaining buds are pulled off, and the umbel is enclosed within a small cheesecloth cage. The inflorescence of the male parent is enclosed within the same cage, with the base of the scape standing in a large test tube filled with water. When handled in this manner, the flowers of the male parent continue to open and to shed pollen for a week or more. Flies are added to the cage. A good supply of them should be kept in the cage to insure thorough pollination.

The above-mentioned technique was advocated by Jones and Emweller (95), (Plates II and III).

Flies belonging to the order Diptera and mostly in the Calliphoridae and Muscidae families were trapped in a special fly-trap placed in an isolated location.

At Baton Rouge seeds were usually planted in the first week of September in small pots of sterilized soil. Seedlings were maintained in the greenhouse until the first week of December, at which time they were transplanted to the field. Some seedlings were set in the greenhouse. Plate I is a general view of the breeding material in the seedling stage.

Thrips, when observed, were controlled by dusting or spraying the plants with DDT.

## INHERITANCE OF RESISTANCE TO DOWNY MILDEW

### A. General Review of Literature

#### Geographical Distribution of the Disease

Downy mildew is present, and often destructive, on onions of various kinds in nearly all parts of the world. It is known to occur in Argentina, Australia, Bermuda, the Canary Islands, China, Denmark, Egypt, England, France, Germany, Holland, Ireland, Italy, Japan, Mauritius, New Zealand, Norway, Russia, South Africa, Spain, and the United States. It has been reported also from Brazil (50), the Philippines (166), and very recently from Peru (176).

In the United States it has been reported from the following states: Arkansas, California, Colorado, Connecticut, Georgia, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, New York, North Dakota, Ohio, Oregon, Pennsylvania, Texas, Vermont, Washington, West Virginia, and Wisconsin (41, 62, 189, 235).

Walker (213) mentioned that onion mildew occurs in the United States most frequently and most severely in the New England States and in New York, Louisiana, California, and Oregon. It is spasmodic in many other onion-growing regions on the bulb crop, the green crop, and the seed crop.

### Common Names of the Disease

As is naturally to be expected, various names have been applied to the disease by growers in different parts of the world. It has been called mildew, mould, blight, white blight, white blast, smut, and rust. Each of the last two diseases is caused by quite a different fungus. The name downy mildew is preferred for mycological and symptomatological reasons (222, 235).

### Economic Importance and Nature of Losses

Berkeley, the first to describe the disease in 1841 in England, stated that it is very common and destructive in some years, preventing the plants which are attacked from coming to perfection (15).

Downy mildew, though sporadic in occurrence, is probably the most destructive disease of onions in the United States. It has been abundant at times in each of the principal bulb-producing states, with the exception of Texas, and in each of the seed-producing states, with the exception of Idaho. The disease frequently spreads rapidly and ruins large acreages, becoming most prevalent under conditions of high humidity (100).

On the crops grown for green bunching or for bulbs, downy mildew infection may significantly reduce the quality and yield of the crop but rarely, if ever, causes complete loss. Obviously the injury to the bulb crop is due primarily to killing of the foliage and consequently reduction in the size of the mature bulbs (100). Observations by Berkeley (15), Whetzel (222), and Cook (41) indicated that

the bulbs of mildewed plants are considerably reduced in size. Taubenhaus and Mally (189) mentioned that, ordinarily, there is little or no increase in the size of the bulbs after a severe infection. If the attack comes after the bulbs are half-formed, it simply means a loss of one-half of the crop. They also stated that experience has taught that it is far easier to prevent its introduction than to attempt to eradicate the disease once it obtains a good foothold in any given field. That statement was made in 1924, and apparently is still true at present.

In considering the nature of injury from onion mildew, sporulation injury is a matter of importance. Yarwood (234) found that the green-weight reduction due to sporulation averaged 55 percent of the green weight of healthy leaves. On heavily-sporulating onion leaves about 10 percent of the stomata were occupied by sporangiophores, and the surface area of the sporangiophores plus sporangia was approximately equal to the area of the leaf surface. The dry-matter content of the sporangiophores plus sporangia produced during one night of sporulation amounted to 5 percent of the dry weight of infected leaves; and this transfer of host nutrients to the fungus is believed to be the feature of sporulation most likely responsible for the injury observed.

Yarwood (234) also noticed that onion leaves on which downy mildew sporulation has occurred die sooner than similarly infected, but nonsporulating leaves. The respiration of infected nonsporulating leaves averaged 69 percent higher than that of healthy leaves, with

the difference highly significant. The respiration of sporulating leaves was 10 percent less than that of nonsporulating leaves, a surprising effect, and the difference was significant.

The disease appears to be the chief handicap to the production of seed onions in Quebec (112). In California the disease is particularly serious in the crop grown for seed. Total loss of seed fields has been observed. Frequently, satisfactory yields are obtained even though the leaves are killed by mildew, but if the scapes are severely infected, the seed yield is reduced (100). In 1935 the disease was severe in all onion fields examined. The greatest damage was to the seed crop, in which 100 percent of the plants were infected and yields were probably reduced 50 percent or more in some cases (232). It was estimated that the loss due to mildew infection in California in the seed crop from 1920 to 1935 has varied from 0 to 80 percent in different years (100).

The reason onion mildew is more serious on the seed crop than on the bulb crop presumably is that the seed plants are exposed to infection for a longer period. If the scapes are injured after the leaves have already been injured or destroyed, no scapes, or very few more, are formed by the plant in an apparent effort at recovery; whereas, if the leaves of plants producing bulbs are destroyed, new leaves may continue to be formed by the uninjured growing point (235). It is believed that onion mildew may reduce the quality as well as yield of seed. The large numbers of shriveled seeds in heads on heavily mildewed scapes is direct evidence of this (235).

In Connecticut, the virulence of the disease varied very greatly, according to the situation of the field attacked, low sheltered ground being the most favorable for its development, while fields located on high land, which admitted of a free circulation of air, were comparatively free from injury. That was the observation of Thaxter and reported in 1889 (190).

Gesun (143), and Doran and Bourne (51) mentioned that the disease caused widespread damage to the onion crop of the Connecticut Valley in 1924, 1925, and 1926. The disease was present in 1927 and 1928 but caused little if any loss in those two years. In 1929, 1930, and 1931, the disease was absent. Tegian (237) stated that prior to 1920 about 90 percent of the onions in the Connecticut Valley were grown from seed and only 10 percent from sets. At present the situation is completely reversed. One of the reasons for this shift is the earlier maturity of the crop, thus avoiding severe inroads of downy mildew.

In 1930 an area in Connecticut was found to be 100 percent infected with mildew. According to Rich and Stoddard (163) this was the first Connecticut report of such a heavy infestation of this disease in the last eleven years.

In 1924 onion mildew was the worst that it had been for several years in New York. It was estimated that there was a 10 percent reduction in yield for the State on account of mildew. In 1935, the disease was present in nine-tenths of the fields inspected. There was some evidence that the fungus had remained viable in the soil without its host plant since the 1932 epiphytotic (138, 139).

Large amounts of onion seed are produced in the Willamette Valley of Oregon. The yield is greatly reduced some years by onion mildew. The economic importance of this seed production and the relation of mildew to yield necessitated the development of an experimental control program during 1937 (125).

In 1945 the disease cost Michigan onion growers an estimated \$2,700,000. Only reductions in yield were considered (6). In 1946 mildew was observed in some fields near Boise, Idaho, with nearly 100 percent incidence and severe damage (106).

A mildew epidemic occurred in the Greeley (Colorado) district the latter part of August 1950 and spread rapidly through the fields. The rapid spread of mildew was made possible by the high relative humidity and cool weather. There was very little rain preceding the epidemic. The leaves of the infected plants were killed, the bulb growth was stopped. Because of mildew, commercial yields were considerably reduced, the tops and bulbs did not mature and cure normally, and heavy losses occurred in storage (58).

In Australia, downy mildew is the most serious fungus disease of onions. In coastal districts the disease usually occurs each spring (8). In Egypt, the disease is destructive in some seasons. In recent years especial emphasis has been laid upon the development of disease-resistant varieties by selection (62).

In England and Wales, Moore (133) mentioned that in years when downy mildew is not generally above normal, at least one-quarter of the onion acreage is affected by it, and about one-sixth is affected by white rot. Observations of McKay (124) under the conditions of Ireland revealed that onion mildew appears more or less every year, often



doing considerable damage to the onion crop by killing the foliage prematurely and preventing the normal development of the bulbs. The bulbs are frequently invaded by the parasite, and in certain varieties the keeping qualities are impaired, the infected bulbs becoming soft and sprouting early.

#### Nomenclature of the Causal Organism

Onion downy mildew was first recorded in 1841 by Berkeley (15), who illustrated and described the conidial stage and named it Botrytis destructor. The perfect stage was not included in this description. In 1860, Berkeley (16) indicated that in view of recently acquired knowledge of the oospores of the group Peronospora, the organism he originally described as B. destructor should be called Peronospora destructor Caspary.

In recent years the nomenclature of the organism inciting downy mildew of onion has been discussed by several workers, including Yarwood (235) and Shaw (177). Shaw indicated that the correct author citation is Peronospora destructor (Berk.) Fries. This binomial is used in the present studies, since it appears to be the proper name of the causal organism according to the evidence presented by Shaw.

The synonymy of Peronospora destructor (Berk.) Fries appears as follows (177, 235):

<u>Botrytis destructor</u>	(Berkeley, 1841)
<u>Botrytis (parasitica?)</u>	(Schleiden, 1846)
<u>Peronospora Schleideni</u>	(Unger, 1847)
<u>P. destructor</u>	(Fries, 1849)

<u>P. destructor</u> Caspary	(Berkeley, 1860)
<u>P. Schleideniana</u> Unger	(De Bary, 1863)
<u>P. alliorum</u>	(Fuekel, 1870)
<u>P. Schleideniana</u> Unger	(Cerna, 1878)
<u>P. Schleideniana</u> De Bary f. <u>espae</u>	(Thuneman, 1879)
<u>P. destructor</u> (Berk.) Caspary	(Wilson, 1914)
<u>P. Schleideniana</u> W. G. Smith	(Wakefield and Moore, 1936)
<u>P. destructor</u> Berk.	(Yarwood, 1943) (235)
<u>P. destructor</u> (Berk.) Fries	(Shaw, 1949) (177)

### History of the Disease

In 1841, Berkeley (15) made the first record of this disease on the leaves of various species of *Allium*, in England. He illustrated the typical conidiophores and conidia of Peronospora destructor known at present.

In December, 1882, Dr. Trelease, Professor of Botany at the University of Wisconsin, announced the finding of the downy mildew fungus attacking onions in a very destructive manner, and included it in the list of the parasitic fungi of the State (205). He described the disease in the first annual report of the Wisconsin Agricultural Experiment Station, published in 1884 (206). It should be pointed out here that downy mildew of onion was first recorded in the United States in 1882, not in 1884 as erroneously mentioned in recent textbooks on plant pathology (28, 213, 215). The disease was observed in New York State in 1888, for the first time.

The first scientific research on onion mildew was done by Shipley (181) in 1857. It was the result of an inquiry conducted under the auspices of the Royal Gardens, Kew, England, into a disease prevalent in the Bermuda Islands affecting the onion crop, which is a staple industry of these islands. Shipley undertook the mission and visited the islands in 1857 to inquire into the causes of a disease prevalent among the onion crop during the preceding seasons, and to suggest remedial measures.

Mr. Arthur Shipley investigated the matter rather thoroughly. He counted the number of stomata and found that the number of stomata is very great, as many as 70,000 exist upon one square inch of onion leaf. If the onion is badly diseased, one of the branching stems of the fungus (conidiophores) will be found projecting into the air through about one stoma in every ten. In some cases two and even three stems may emerge from one stoma, so that on a square inch of a diseased onion leaf we may fairly estimate the number of stems (conidiophores) as almost one-tenth of the number of stomata, that is, 7,000. If we take 20 as the average number of spores upon one stem, and that is rather below than above the average, we find that a single square inch of a diseased onion leaf may have the enormous number of 140,000 spores, each capable of reproducing the fungus, and hence the disease.

Shipley also mentioned that the atmospheric conditions which favor the progress of the disease are heavy dews or rains followed by warm, moist, calm weather, and the absence of direct sunshine and cold winds. In favorable weather the progress of the disease is very rapid.

In 1904, Whetzel (222) gave the most complete account of the disease that had been published up to that time. In 1939, Jones, Porter and Leach (100) published their investigations on breeding for resistance to onion mildew. It is considered the most comprehensive reference on that subject. In 1943, Yarwood's studies on downy mildew of onion were published (235). In his extensive studies he reported the tests conducted to control the disease by the use of fungicides.

#### Occurrence of the Disease in Louisiana

Once again the work of the pioneer phytopathologist in the South, Dr. Edgerton, is distinct. In 1914 there was an article on the onion mildew that came from Our Department. It was one of the earliest publications on this disease (57).

In 1917, Edgerton (53) reported that the yield of dry onions was much decreased and the seed crop was generally almost a total loss on account of mildew. In his interesting reference in 1921 (54) the following statements are recorded:

"For a number of years onion diseases have been causing considerable injury in some sections of South Louisiana, being particularly severe in the Bayou Lafourche region, the most important onion section of the State. In most cases, an outbreak of onion mildew is quickly followed by the black stalk rot (Macrosporium parasiticum). The mildew has never been seen on the high land at Baton Rouge, although during three years bulbs were brought from the infested region along Bayou Lafourche and planted."

Dr. Edgerton was wondering in the statement: "Whether the mildew will develop in the high land at Baton Rouge as well as it does in the alluvial sections, is still a question."

In a review of the work in Our Department, published in 1951, Edgerton (56) mentioned that in the years between 1918 and 1921, a survey was made to determine what diseases of the onion were present and attempts also were made to control the mildew with sprays. The waxy surface of the leaves prevented proper coverage with the sprays and the results obtained were not considered satisfactory.

In 1924, the disease was present but not troublesome (55). In 1941, Forbes (64) reported on the epidemic of that year, saying that the disease was responsible for the abandonment of the commercial production of onions in Lafourche Parish about 20 years ago, and growers were again very pessimistic over the future of the industry.

Since 1943 reports and investigations of Dr. Tins on the downy mildew have been continuous. The disease occurred in epiphytotic proportions in Louisiana in 1943, being much more severe than in 1941, when it caused severe losses. The epiphytotic was confined to the lower Mississippi River and the Bayou Lafourche region (192). In 1944 it was of minor importance (193). In the spring of 1946, a destructive epiphytotic developed in Lafourche and Terrebonne Parishes, two of the most important onion-producing parishes (194). In the spring of 1947 the disease occurred in widespread and destructive form in southern Louisiana. The disease caused more severe damage over a wider area than in any previous season for many years. One planting of stock seed of a selected strain of Greole was completely wiped out on the Experiment Station grounds at Baton Rouge (196). In 1948 the disease was not observed, but it did occur early in 1949 (198). Mildew epiphytotic occurred in 1949 and 1950. In 1951 the disease was present but did not cause any appreciable damage to the commercial crop.

Writing in 1950, Tins (201) described the onion mildew as the most important disease of onions grown for bulbs and for seed in the southern part of the state. He mentioned that during the last 20 years onion downy mildew has developed sporadically in Louisiana. During that period, almost every third year the disease caused serious damage to the onion crop. But in the last four years, 1947-50 inclusive, there have been three very destructive epidemics. In fact, mildew has caused such serious losses that some farmers who have grown onions for many years have given up the crop completely (200).

In 1950, Andersen, the Commissioner of Agriculture in the State of Louisiana, stated that onion mildew was costing the State more than a quarter of a million dollars a year. Unless mildew is stopped, Louisiana farmers will no longer be able to grow shallots or onions (3).

### Symptoms

Symptoms of the disease were described under the conditions of New York, California, and in general by Cook (41), Yarwood (235), and Walker (215), respectively. In Louisiana, Tins (201) mentioned the disease symptoms. Observations made in the onion experimental plot in the last two growing seasons lead to the following descriptions of onion downy mildew symptoms.

The first sign of the disease on early-infected plants is the production of conidiophores a short distance back from the tips of the older leaves. The conidiophores have a purplish tinge when fresh, and give the lesions a downy mildew appearance. Soon the affected part of

the leaf turns yellow, withers and breaks over. Afterward the fungus may fruit at any time on the leaves, with the same ultimate results--the death of the affected tissues.

Conidia disseminated by air result in secondary infection and spread of the disease. Local lesions resulting from secondary infection are oval to cylindric in shape, variable in size, and often paler than the normal green color of the tissues of the leaf or of the scape. In humid atmosphere the lesion may become necrotic in the center without fructification. Infected tissues may die without the occurrence of sporulation, but the latter hastens the death of infected tissues.

The severity of the disease depends on the environment. Advance may be checked for a time in dry weather and then be renewed with the return of moist conditions. In cases of heavy infection, the leaves are progressively killed back to the leaf sheath. As the growth of onion leaves is from the base, infected tissues on these leaves are being pushed farther away from the base of the plant, and as the infected tissues die a tip-blight condition of the leaves becomes apparent.

When expanding scapes are infected, uneven stunted growth follows. When growth is checked by infection on one side of the scape, the latter bends in the direction of the lesion. In some cases, the lesions are large and girdle the scape. Infected areas are distributed throughout the length of the scape and mildew lesions of various sizes and shapes often cause the scape to break over. In wet weather, mildew lesions are soon invaded and overrun by a secondary organism identified as Macrosporium parasiticum Thum. The lesions then become

brownish black. This stage was called by Edgerton (54) the "black stalk rot disease". Sometimes it is called leaf mold. Walker (215) mentioned that leaf mold disease is a widespread one which commonly follows mildew or purple blotch (Macrosporium porri). The incitant is a very low grade parasite and does little or no damage independently. In lesions already incited by the mildew it thrives and fruits abundantly, the dark spores causing a black moldy surface. The latter often obscures the presence of the primary pathogen. Walker continued: "It is doubtful whether leaf mold causes any real damage to onion." The causal organism is Stemphylium botryosum Wallr. (synonym. Macrosporium parasiticum Thum.). The ascigerous stage is Pleospora herbarum (Pers. ex Fr.) Rab. (215).

Yarwood (235) stated: "Infection with Macrosporium has followed that with downy mildew on onion leaves and seedstalks in the field each year from 1935 to 1940, though I have not observed Macrosporium on leaves or seedstalks not already infected with downy mildew."

In Ireland, McKay (124) noticed that in the growing onion the mildew fungus may exist for weeks, or even months, without any external indications of its presence. Under certain conditions no external symptoms of the fungus may be visible, but when it reveals itself by the production of conidia the host cells rapidly die over the area where fructification has occurred. The presence of the oospores is frequently indicated by rusty, reddish-brown areas on the foliage, the tissues often becoming sunken. Oospores are not formed on mildewed plants every year, but one year's crop of them may contaminate the soil for a long period--exactly how long is not known.



Under the conditions of the Philippines, mildew caused necrotic oval-oblong lesions in both the leaves and scapes, causing their ultimate death. This is particularly damaging to the scapes, as it prevents the seed from coming to maturity. The disease is initiated by Peronespora destructor and followed by a persistent invader, Macrosporium sp., which greatly hastened the death of the plants (166).

An epiphytotic of downy mildew in an onion field compared with a healthy field, symptoms of mildew on foliage and on scapes are illustrated in Plates IV, V, VI, VII, and VIII.

#### Disease Cycle

The method by which downy mildew started in the onion experimental plots has not been investigated. However, in February, 1951, there was an evidence of mycelium carried over by diseased bulbs from the preceding 1950 epiphytotic. Infection centers apparently started from a few scattered bulbs which harbored the mycelium.

Murphy (135) found the mycelium of the mildew fungus in the bulbs of the common onion and of the shallot. It was proved also that the mycelium survives when infected bulbs are left in the soil during the winter. Murphy and McKay's discovery of the mycelium of Peronespora destructor in the bulbs of topset onions (136) was confirmed by Newhall (140).

In 1944, in Denmark (5) downy mildew was widespread on onions and shallots, infection originating on the latter host. In 1946, mildew was widespread on shallots in Louisiana (195) in the same general

areas where it occurred on onions. It seems quite probably, according to Fims (195), that the mildew fungus may be carried through the summer and fall on shallot, either while green in the field or on the dry tops in storage.

Yarwood (235) stated:

"Of the four principal methods by which onion mildew might originate, namely, 1-systemic mycelium in the bulbs, 2-cosperes in soil or refuse, 3-sporangia from regions where onion mildew prevails through the year, and 4-infected seed, I believe the first is of greatest importance in California, the second two are of minor importance, and the fourth is of very little importance or nonexistent."

The mycelium of the fungus was found in abundance in the flower pedicels, petals, stamens, ovary, and ovules. Cook (40) was the first to reveal the presence of the mycelium in the ovules, and he concluded that this indicates that it is also present in the mature seed (e.g. seed coat). Hura (76), who found abundant hyphae within the tissues of the flower stalks, perianths, styles, ovaries, filaments, and anthers, did not notice any infection which resulted from seeds obtained from diseased plants.

The conidia (sporangia) of Peronospora destructor germinate by means of one or two germ tubes. The germ tube usually forms an appressorium over the stomatal opening, penetrates through the stoma, and forms a substomatal vesicle from which the intercellular mycelium arises and sends filamentous haustoria into the host cells.

Conidia are produced in high humidity, the minimum about 90 percent, over a range of 4 to 25° C., with an optimum at about 13° C. Conidia develop during the night, maturing early in the morning and being disseminated during the day. Both relative humidity and alter-

nation of light and darkness influence sporulation. The conidia remain viable, when attached, for about 3 days, or even longer in the dark, but for a shorter period when detached. Air dissemination is the chief means of spread. Germination occurs in water from 1 to 28° C. (215, 235).

From data of the time required for sporulation, germination, and penetration, Yarwood (235) believed that 2 humid nights are usually necessary—1 humid night for sporulation, 1 day period for dissemination of conidia and 1 night with free moisture on the leaves for germination and penetration.

Relatively cool and rather humid weather is required to build up an epiphytotic. Rain is not necessary if heavy dews occur repeatedly. Yarwood (235) suggested that the epidemiological factors critical in determining the incidence and severity of onion mildew in California are, in order of importance: source of inoculum, temperature, moisture conditions, and wind.

The imperfect stage of Peronospora destructor (Berk.) Fries, briefly described in the preceding paragraphs, is very noticeable. The sexual stage is discussed by Whetzel (222) in detail and has not been found during the present studies. Oospores were first reported in the United States by Jones (102) in 1895. In 1897, he indicated that the fungus lives through the winter by means of resting spores (oospores). These spores pass into the soil where the blighted onion leaves are allowed to remain in the field, and upon germinating the following spring start the disease anew if onions are again planted on that soil. The fact of this soil infection was clearly shown by greenhouse experiments conducted during 1895-96 (103).

Newhall (140), the first to record the aerial dissemination of the conidia of P. destructor, presented proof that the conidia can be recovered from the air several hundred feet off the ground in a viable condition and that the spores are well able to remain viable for several days at temperatures and humidities that often prevail in the spring for many days in the Northeastern States. Yarwood (235) stated that the distribution of onion-mildew infection in several California fields afforded good circumstantial evidence of the wind-borne nature of the disease.

To obtain an idea regarding the potential number of spores that a diseased spot could produce, the following counts and computations were made by Newhall (140).

The number of stomata per square inch of onion leaf surface was found to be approximately 65,000. If we then postulate 1 conidiophore growing out from 1 of every 10 stomata, we have a total of over 100,000 conidia per square inch of leaf surface. It is, of course, common for the fungus to sporulate over several square inches of a plant at one time, so that a single small planting of a few dozen diseased onions can give rise to many millions of conidia overnight and can repeat this production many times in case of an epiphytotic. Newhall also mentioned that he has wiped a crop of conidiophores from a given leaf (from the same area) as many as 3 times, and each time a new crop formed within 48 hours (140).

The results of some interesting experiments carried out by Yarwood (235) indicate that onion leaves, outdoors at night or in dark moist chambers, generally registered a lower temperature than that of the surrounding atmosphere. This lower leaf temperature, in a humid

atmosphere, is believed to be primarily responsible for the condensation of moisture on the leaves and the consequently favorable conditions for infection. Relatively little moisture condenses on the normally erect leaves; on inclined or horizontal leaves, however, there may be heavy condensation on the upper surface, with very little on the lower. Under these conditions considerable spread of the disease may occur. In a review of the detached leaf culture, Yarwood (236) mentioned that penetration of onion by Peronospora destructor was readily followed on detached leaves. However, detached leaves have not been successful as a culture medium of this fungus. Detached onion leaves usually died in about four days, a period too short for the satisfactory culture of almost any pathogen.

Murphy and McKay's contributions to some phases of the disease are outstanding (136, 137). Spraying the foliage with conidia produced the mildew, and in turn the bulbs became infected with mycelium. The mycelium was found invading the fleshy scales and the stem. The appearance of mildew on the shoots that developed from infected bulbs in the following spring was repeatedly demonstrated and clearly indicated the perennial nature of the mycelium. The oospores were shown to survive in the soil in an ungerminated state for at least three years. Proof was obtained that naturally contaminated soil freely conveyed the mildew to seedling onions.

### Host Range

Peronospora destructor (Berk.) Fries has been reported on the following hosts (41, 235), the scientific names of which are copied from Bailey (9):

<u>Allium ascalonicum</u> L.	(Shallot)
<u>A. Ceba</u> L.	(Onion)
<u>A. Ceba</u> var. <u>aggregatum</u> Don.	(Potato or Multiplier onion)
<u>A. Ceba</u> var. <u>viviparium</u> Metz.	(Top onion)
<u>A. fistulosum</u> L.	(Welsh Onion)
<u>A. nigrum</u>	
<u>A. oleraceum</u>	
<u>A. Porrum</u> L.	(Leek)
<u>A. sativum</u> L.	(Garlic)
<u>A. Schoenoprasum</u>	(Chives)
<u>A. ursinum</u>	

### Research on Disease-Resistant Varieties

Efforts to control onion downy mildew by the use of fungicides have not been successful.

Writing in 1911, Smith and Smith (184) mentioned that the disease had not been successfully controlled in California. The development of resistant strains by seed selection was promising. Information available in 1917 did not warrant the spraying of onions in New York State. The cost of spraying onions was high, and the control of the disease had generally been unsatisfactory (81). Dr. A. G. Newhall,

who furnished the material on diseases included in Knott's bulletin (107) published in 1930, mentioned that each year a few growers in New York State tried spraying or dusting with a copper fungicide, but no satisfactory control had been obtained. According to Cook (41) fungicidal treatment was not considered a satisfactory method of control. In order to protect the plant properly, it would be necessary to begin spraying or dusting in the seedling stage and to continue the treatment until shortly before harvest. This would make the cost of growing onions prohibitive. In 1944, Rader and Ashdown (156) stated that onion mildew was present nearly every year in New York, and was destructive in 2 or 3 years out of 5. No spray or dust program has ever given effective control on the onion bulb crop in this area.

Yarwood (232) in 1935 stated that fungicidal sprays have in general given unsatisfactory results in California. In 1943 he published the results of his extensive studies on the control of onion mildew and on several other phases of this disease (235). As he put it "reports of investigations of fungicidal control are so fragmentary, contradictory, and so poorly supported by data, that a reader (of these early investigations) might appear safe in concluding that fungicidal control of onion downy mildew has never been adequately demonstrated". Yarwood adequately demonstrated the fungicidal control of mildew and reached the following conclusions:

"The methods that appear most promising for offsetting the danger from onion mildew are: the development of mildew-resistant varieties, the avoidance of disease, the production and storage of sufficient seed in seasons when the disease is not severe to make up for losses during seasons of mildew severity, and the use of protective sprays. Protective sprays should be used to supplement the other control methods."

Some of Yarwood's observations were that onion leaves and scapes elongate principally at the base, and the younger leaves may grow very rapidly. This growth from the base makes protection with fungicides more difficult. Onion leaves are not readily wetted by ordinary solutions or water suspensions, and this difficulty of wetting increases the difficulty of depositing a protective covering on the leaves.

Levallee (112) in Canada conducted spraying tests using some of the formulas put forward by Yarwood (235), but he noticed that the disease was as severe on the sprayed as on the unsprayed plants. Almost all the scapes were affected and 75 to 80 percent of the crop was lost.

In 1943, Flakidas (149) stated that control of onion mildew was extremely difficult. Spraying had been tried in the past, both in Louisiana and in other onion-growing states, but it had not proved very satisfactory. To obtain good control it was necessary to keep the new growth covered with spray material as soon as it developed. This meant spraying at least once a week for several months. Obviously such a procedure was economically impractical. Tins (200), in 1950 mentioned that attempts were made to control onion mildew in Louisiana by the use of fungicides as early as 1919. Results revealed that the final solution to this disease problem in Louisiana seemed to be the development of resistant varieties (197, 200, 202).



It is mentioned in a recent publication (36) in Great Britain that no satisfactory method of controlling onion mildew by spraying has yet been devised and the disease must be avoided as far as possible by preventive measures.

Chapp (34) and Chapp and Leily (35) stated that much has been written regarding the spraying of onions for the control of mildew. At best spraying is a difficult task, and so far it has not proved profitable. Very recently, Walker (215) stated:

"Although many control experiments with organic and inorganic fungicides show a reduction in the amount of disease, control by these means has seldom been applied successfully. Factors which seem to have reduced the effectiveness of this type of control measure are the spasmodic nature of the disease, the difficulty in getting fungicides to stick on the glossy surface of onion leaves, and the rapid exposure of new leaf tissue during the growing period."

The need for the development of mildew-resistant varieties is quite evident, since the fungicidal control was almost a failure. In 1887, Shipley (151) stated that the disease attacks both red and white varieties of onions indifferently, but the former resist it slightly better. That claim was made under the conditions of the Bermuda Islands. In New York, Cook (41) tested fifty-three varieties under field conditions, and practically 100 percent of the plants became infected.

Felix (60) found that the Winterhecke variety (Allium fistulosum) showed a seeming degree of resistance to mildew, in that infections were confined to relatively small local areas and did not spread readily over the entire leaf surface.

In Michigan the main breeding endeavor has been aimed at finding surviving onion plants in fields which have been scourged by mildew epiphytotics. It has been stated, without any presentation of data, that this method was producing encouraging results and distinct progress has been made in obtaining resistant lines (6).

Observations on varietal reaction to the disease in Ireland indicated that Cranston's Excelsior and Up-to-Date were both resistant in the foliage. Up-to-Date was also resistant in the bulbs. Bedfordshire Champion and James's Keeping were susceptible in the foliage, but the bulbs of the former consistently showed fair resistance (136, 137).

In breeding for resistance to downy mildew, Italian Red 13-53 has come to our aid. Its high resistance to this disease was first observed in 1934 in the breeding plots at Davis, Calif. Under California conditions, infection is usually confined to the tips of the leaves, and the spread toward the base is slow. The scapes of 13-53, however, are immune. Lesions have never been found even during the most severe epiphytotics. It is considered to be the best source of resistance to downy mildew (91).

It has been shown (141) that the so-called scape resistance to mildew derived from the Italian Red 13-53 was not effective in saving the leaves from heavy attack in New York. Consequently, the work on mildew resistance has since been concentrated on the west coast, where scape resistance is of much greater importance than in New York.

In breeding onions resistant to downy mildew the progenies are tested in localities that are most congenial for the development of the disease. One such place is in California near the southern end of

San Francisco Bay. Here climatic conditions are ideal throughout most of the year for the spread of the disease, and there is very little opportunity for susceptible plants to escape infection (25).

At the present time breeding for resistance to downy mildew seems to be confined to California and Louisiana.

#### Research in California:

The earlier observations by Jones (84) indicate that the foreign types, like Giant Gibraltar, Sweet Spanish, Prisetaker, and others with light green tops, appear to be somewhat more resistant to mildew than the storage varieties like Yellow Globe Danvers and Southport. Rosa (168) observed that the leaves and scapes of the white varieties were attacked earliest and most severely. Field experiments conducted by Yarwood (235) on the relative mildew susceptibility of several onion varieties indicated that Italian Red 13-53 produced immune scapes and only 2 percent foliage infection. Among varieties more tolerant to mildew were Australian Brown, Utah Sweet Spanish, and Ebenezer.

Greenhouse tests to determine the relative susceptibility of onion varieties were reported once in the literature. These were conducted by Yarwood (235) and were neither extensive nor highly successful.

There is only one comprehensive reference on breeding for resistance to onion mildew. This was made by Jones, Porter and Leach (100). The results of this cooperative investigation conducted by the United States Department of Agriculture Bureau of Plant Industry and the California Agricultural Experiment Station were published

in 1939. They presented data relative to varietal reaction to mildew, discussion of resistant types that have been found, and the status of the breeding work designed to transmit resistance to varieties of commercial importance. Because of the importance of this reference it is reviewed here in detail.

Comparisons of susceptibility were made in 1934 on a number of commercial varieties and foreign introductions. Among the most susceptible were Crystal White Wax, Yellow Bermuda, Red Creole, Lord Howe Island, Nebuka (A. fistulosum), White Persian, and most of the foreign plant introductions. All hybrids between Allium fistulosum and A. Cepa were extremely susceptible. Resistance tests continued through 1936, using commercial varieties and different crosses.

Three sources of resistance have been found. The most promising is Italian Red 13-53 in which the scapes are immune and the foliage is highly resistant. Italian Red 13-20-3 likewise manifests scape immunity, but the foliage is only slightly resistant. Scape immunity was also found in an  $F_1$  hybrid between Red 21 and two inbred lines of Steckton Yellow Flat, namely, 50-6 and 50-6-1. Since 13-53 and 13-20-3 represented bulbs from the same population of Italian Red, it is evident that there existed in this lot of seed the gene or genes for resistance to downy mildew. Small mildew-like lesions frequently occur on scapes of 13-53 and 13-20-3, but sporulation has never been observed and microscopic examination of cross sections of such material has never revealed either mycelium or haustoria.

In 1937, the reaction of the various  $F_1$  hybrids seemed to indicate that scape resistance was inherited as a dominant character and that the resistant parent (13-53) was heterozygous for resistance. In 1938 many  $F_1$  populations between susceptible varieties and 13-53 appeared to be about equally resistant to foliage reaction, being intermediate between the two parents. Backcrosses were made to develop mildew-resistant strains typical of the various varieties. These populations, backcrossed to the susceptible parents, had many plants in the immune and highly-resistant classes.

Lord Howe Island (one of the parents of Calred) was susceptible in foliage and scapes. Jones and his associates followed a scheme to describe the degree of infection in the scapes. The scapes were indexed according to an arbitrary rating from 0 to 10. The rating of 0 indicated the most severe degree of infection. Damage was of strictly minor importance until the stage represented by a rating of 4 was reached. From a breeding standpoint, plants rating 1 or 2 are almost as valuable as those which merit a rating of 0, and only those plants manifesting stage 4 or higher are considered as suffering from mildew injury. These investigators finally stated:

"Before the definite mode of inheritance can be determined, the seedstalks of borderline plants will probably need to be examined microscopically to determine definitely in what classes they belong. Also, some means must be established to determine the number of scapes in the apparently immune class." (100)

For the development of mildew-resistant types, the general procedure has been to cross 13-53 with selected individuals from standard commercial varieties, select male-fertile, resistant in-

dividuals from the progeny and backcross to the recurrent or commercial parent. Generally 2 or 3 backcrosses are sufficient to allow for selection of individuals for all practical purposes the same as the commercial parent. After this, one or more generations were grown by selfing selected resistant individual plants. Finally, several closely-related lines may be massed to regain vigor (43). Mildew readings are made on the scapes. The first mildew-resistant variety secured by the above procedure was Calred. It is a cross between 13-53 and Lord Howe Island.

Recent results, reported by Davis (14, 15) indicate that Crystal Wax check plants were completely destroyed. Three lines involving Red 21, Early Crane, and Yellow Globe Danvers were sufficiently resistant to warrant their increase for mass seed production tests in the Milpitas district.

#### Research in Louisiana:

Under the leadership of Dr. Miller (126) the horticultural investigational work started in August, 1929, and the project of selection and breeding of the Creole began. In 1941-42 the strain G 5 of the Red Creole was released. It is more uniform in shape and color (35). The quantity of seed of this strain produced by Louisiana growers in 1948 was five thousand pounds (130). In 1949 this was reduced to 950 pounds (131), and the chief cause for this tremendous loss was the mildew epiphytotic.

Time (197) mentioned that a new project on breeding for disease resistance in shallots and onions was started in 1948. Nothing was published before 1948 on testing onion varieties for disease re-

sistance in Louisiana. The program is under way between the United States Department of Agriculture (The National Onion-Breeding Program) and the Louisiana Agricultural Experiment Station. Results accomplished during the period 1945-1951 were published (203, 204, 216, 217) and are reported in this dissertation in detail.

## B. Experimental Methods

There was a natural epiphytotic of mildew in the 1949-50 season. A record on the degree of foliage infection was taken in this season for the parental varieties, 22  $F_1$  plants and 5142  $F_2$  plants. Although the season of 1950-51 was dry, the disease was present. Because of the unfavorable weather conditions (especially the low relative humidity) the disease did not spread evenly. An effort had been made to produce an artificial epiphytotic by operating a water-sprinkling system in the evenings. The result was the spread of mildew as well as some secondary organisms (e.g. Macrosporium parasiticum Thum.) which attacked the infected scapes. The susceptible scapes soon fell down, blackened and died because of the mildew disease complex. Red Creole bulbs were interplanted among the  $F_2$  populations to aid in the production of the inoculum. The record of the degree of scape infection was based on two classes of reaction. Susceptible scapes fell down and died while resistant ones were unaffected. This record was taken for 5  $F_1$  plants, 603  $F_2$  plants, and for 36 plants of the first backcross generation. Populations of the  $F_2$  generation, used for this record, were only those which exhibited a high degree of bolting. The Calred plants grown even from bulbs, did not produce scapes during the two seasons. On the other hand the Red Creole bolted freely.

The chi-square test was used for determining goodness of fit of observed data to conventional Mendelian ratios.



An attempt was made to identify the downy mildew strain prevalent in the southern part of Louisiana. Naturally-infected onion leaves were collected at different intervals, especially those from Baton Rouge. Conidial water suspensions were made soon after bringing the specimens to the laboratory. A fairly large number of conidia (200 or 300 conidia) from each source was measured. From a single conidial mount, approximately 10 conidia were measured under the high power of the microscope ( $\times 450$ ). The measurements were subjected to statistical analysis.

Table XVI. RECORD OF BULB COLOR IN F<sub>2</sub> POPULATIONS GROWN AT  
BATON ROUGE, LA. AND AT GREELEY, COLO. (G-LOTS) -  
1950

Lot	Distribution with- in color class:						N	Ratio II, III, IV: I	P
	I	II	III	IV					
Calred x Red Greele									
100	944	945	4	24	89	793	910	255:1	.80-.90
100-0	"	"	1	10	68	144	223	255:1	.80-.90
101	"	"	3	22	92	561	678	255:1	.80-.90
101-0	"	"	0	20	61	81	162		
102	946	945	12	23	79	125	239	15:1	.30-.50
102-0	"	"	2	8	44	47	101	15:1	.05-.10
103	"	"	5	13	82	123	223	63:1	.30-.50
103-0	"	"	0	6	18	13	37		
108	950	945	15	35	51	185	286	15:1	.30-.50
108-0	"	"	10	34	87	71	202	15:1	.30-.50
109	"	"	9	43	198	372	622	63:1	.80-.90
109-0	"	"	0	9	73	203	285		
110	"	"	2	20	84	219	325	255:1	.50-.70
110-0	"	"	0	3	36	80	119		
111	"	"	20	45	98	218	381	15:1	.30-.50
111-0	"	"	0	0	11	56	67		
112	"	"	2	18	28	57	105	63:1	.70-.80
112-0	"	"	0	1	11	21	33		
113	"	"	1	26	96	222	345	255:1	.70-.80
113-0	"	"	0	2	42	74	118		
Red Greele x Calred									
104	949	946	18	51	115	109	293	15:1	.90-.95
104-0	"	"	1	3	21	37	62	15:1	.10-.20
105	"	"	13	31	106	82	232	15:1	.50-.70
105-0	"	"	2	21	33	29	85	15:1	.10-.20
106	"	"	5	49	131	147	332	63:1	.90-.95
106-0	"	"	2	15	71	74	162	63:1	.70-.80
107	"	"	20	77	81	60	238	15:1	.10-.20
107-0	"	"	1	1	17	53	72	15:1	.05-.10

\* Class I-light red. II, III-intermediate. IV-dark red

with susceptibility dominant. Four of the eleven  $F_2$  populations segregated into ratios which were a good fit to 3 susceptible to 1 resistant (Table II).

On the basis of the segregating generation ( $F_2$ ) the assumption is made that the Calred plants possessed two duplicate genes for resistance. These genes, tentatively designated  $s_1$  and  $s_2$ , are independently inherited. Each gene is recessive to its allele for susceptibility,  $S_1$  and  $S_2$ , respectively. The Calred parent is assumed to have the genetic constitution  $s_1s_1 s_2s_2$ .

Due to the fact that the Red Creole parent is highly susceptible to mildew, and the non-existence of any resistant scapes among the 130 Red Creole plants observed in the 1950-51 season, it is assumed that this parent is homozygous for either  $S_1$  or  $S_2$  or both. Possible genotypes of the Red Creole parent were  $S_1S_1 S_2S_2$ ,  $S_1S_1 s_2s_2$ ,  $s_1s_1 S_2S_2$ ,  $S_1s_1 s_2s_2$ ,  $s_1s_1 S_2s_2$ . Only two Red Creole plants (i.e. 945, 949) were involved in the crosses. Each of these gave both 3:1 and 15:1 ratios in  $F_2$ . There were only two genotypes, out of the five possible ones listed above for the Red Creole, which could give both 3:1 and 15:1 ratios in  $F_2$ . These were  $S_1S_1 S_2s_2$  or  $S_1s_1 S_2S_2$ .

The above assumptions would explain the reason for obtaining ratios of 3:1 (in four  $F_2$  populations) and 15:1 (in six  $F_2$  populations). Table III shows a factorial analysis of the parents and eleven  $F_2$  populations, on the basis of a two-factor difference. Only plants with the genotype  $s_1s_1 s_2s_2$  are resistant.

In one  $F_2$  population (lot 109), there were no resistant scapes found irrespective of the large number of scapes examined. This population is a progeny of a sister plant in the cross 950 x 945 in which ratios of 3:1 and 15:1 were found. It seems possible that through chance there was a failure to obtain resistant scapes in this  $F_2$  population of 101 plants in which a ratio of 15 susceptible to 1 resistant was to be expected.

Highly resistant scapes have not been found in any of the first backcross populations. However, scapes with one or few small mildew lesions were noticed and these were classed as moderately resistant. Some plants produced susceptible scapes which soon fell down and died.

In the two 1st backcross populations, segregation appeared to fit a ratio of 3 susceptible to 1 moderately resistant. The P values were between 0.50 and 0.95 (Table IV). Under the hypothesis that Red Creole is  $S_1S_1 S_2s_2$  or  $S_1s_1 S_2S_2$  and Calred is  $s_1s_1 s_2s_2$ ,  $F_1$  plants would be  $S_1s_1 S_2s_2$  and  $S_1s_1 s_2s_2$ , hence susceptible. The progeny resulting from backcrossing  $F_1$  plants of the genotype  $S_1s_1 s_2s_2$  to Red Creole ( $S_1S_1 S_2s_2$ ) would be of the following genotypes:

3 susceptible : 1 moderately resistant

$S_1S_1 S_2s_2$

$S_1s_1 s_2s_2$

$S_1s_1 S_2s_2$

$S_1S_1 s_2s_2$

None of these genotypes would be as highly resistant to Calred ( $s_1s_1 s_2s_2$ ). Thus, the results from backcross populations are in accord with the hypothesis to account for inheritance of resistance.

In general, the  $F_2$  data, supported by first backcross data presented in this study, have brought about a strong indication for the existence of two duplicate recessive genes for resistance present in the Calred plants. Before it is assumed to be proved it should be confirmed by  $F_3$  data.

The association between the degree of foliage infection and scape infection in  $F_2$  populations was measured by calculating the correlation coefficient ( $r$ ). In lot 101 the  $r$  value was equal to .221. Though it is significant, it is too small to indicate an important association between the two characters. In lots 102 and 110, the correlation was positive but non significant. In lots 104 and 111, the correlation was negative but non significant also. The average correlation coefficient in the material studied, as a whole, was found to be .111 and not significant. It was concluded that no association exists between the degree of foliage infection and that of scape infection, in the material studied (Table V).

Table I. REACTION OF FOLIAGE TO DOWNY MILDEW  
IN PARENTS AND F<sub>2</sub> POPULATIONS - 1950

Lot	Pedigree		Plants tested	Plants resistant	% plants resistant
			Number	Number	
Calred x Red Greole					
100	944	945	910	220	24.2
101	"	"	668	43	6.4
102	946	945	241	33	13.7
103	"	"	222	19	8.5
108	950	945	287	8	2.8
109	"	"	624	45	7.2
110	"	"	325	31	9.5
111	"	"	352	50	14.2
112	"	"	105	12	11.4
113	"	"	332	14	4.2
Red Greole x Calred					
104	949	946	293	28	9.5
105	"	"	232	22	9.5
106	"	"	330	33	10.0
107	"	"	221	15	6.8
Red Greole			109	0	0.0
Calred			56	56	100.0

Table II. REACTION OF SCALES TO DOWNY MILDEW  
IN PARENTS AND F<sub>2</sub> POPULATIONS - 1951

Lot	Pedigree		Number of plants		Ratio	P
			Suscept.	Resist.		
Calred x Red Creole						
100-C	944	945	66	7	15:1	.20-.30
101	"	"	142	7	15:1	.30-.50
102	"	"	11	6	3:1	.30-.50
103	"	"	19	7	3:1	.80-.90
108	950	945	61	3	15:1	.50-.70
109	"	"	101	0	----	
110	"	"	31	1	15:1	.30-.50
111	"	"	23	4	3:1	.20-.30
113	"	"	24	1	15:1	.50-.70
Red Creole x Calred						
104	949	946	36	13	3:1	.80
106-C	"	"	38	2	15:1	.70-.80
Red Creole			130	0	----	
Calred			----	-	----	

Table III. FACTORIAL ANALYSIS OF ELEVEN F<sub>2</sub> POPULATIONS OF ONION HYBRIDS  
ON THE BASIS OF A TWO-FACTOR DIFFERENCE IN PARENTS

Lot	Pedigree		Ratio S:R	Possible genotypes of the Red Greole parent*
	Calred x Red Greole			
100-C	944	945	15:1	$S_1S_1 S_2S_2$ , $\frac{S_1S_1 S_2s_2^{**}}{s_1s_1 S_2S_2^{**}}$ , $\frac{S_1s_1 S_2S_2^{**}}{s_1s_1 S_2S_2^{**}}$
101	"	"	15:1	"
102	946	945	3:1	$S_1S_1 s_2s_2$ , $\frac{S_1S_1 S_2s_2^{**}}{s_1s_1 S_2S_2^{**}}$ , $\frac{S_1s_1 S_2S_2^{**}}{s_1s_1 S_2S_2^{**}}$ , $s_1s_1 S_2S_2$
103	"	"	3:1	"
108	950	945	15:1	$\frac{S_1S_1 S_2s_2^{**}}{s_1s_1 S_2S_2^{**}}$ , $\frac{S_1s_1 S_2S_2^{**}}{s_1s_1 S_2S_2^{**}}$
109	"	"	Suscept.	"
110	"	"	15:1	"
111	"	"	3:1	"
113	"	"	15:1	"
	Red Greole x Calred			
104	949	946	3:1	$\frac{S_1S_1 S_2s_2^{**}}{s_1s_1 S_2S_2^{**}}$ , $\frac{S_1s_1 S_2S_2^{**}}{s_1s_1 S_2S_2^{**}}$
106-C	"	"	15:1	"

\* Genotype of Calred assumed to be  $s_1s_1 s_2s_2$ .

\*\* Most probable genotypes



Table IV. REACTION OF SCALES TO DOWNY MILDEW IN 2 FIRST  
BACKCROSS POPULATIONS - 1951

Lot	Pedigree	Number of plants		Ratio	P
		Suscept.	Mod. resist.		
La 16	F <sub>1</sub> (1696)* x Red Creole	20	7	3:1	.92-.95
La 17	F <sub>1</sub> (1706)* x Red Creole	6	3	3:1	.50-.70

\*The original cross is Red Creole (949) x Calred (946).

Table V. THE CORRELATION BETWEEN THE DEGREE OF  
FOLIAGE INFECTION AND SCAPE INFECTION  
IN FIVE F<sub>2</sub> POPULATIONS

Lot	Pedigree		r
	Calred x Red Creole		
101	944	945	.221*
102	946	945	.208
110	950	945	.234
111	"	"	-.198
	Red Creole x Calred		
104	949	946	-.152
101, 102, 110, 111 & 104			.111

\* Significant at .05 level

Conidial measurements:

Range of the width of conidia collected from different localities is given in Table VI. Range of the length was 40.7 to 72.1 u, 48.1 to 77.7 u, and 46.2 to 77.7 u for conidia collected from Baton Rouge, Labadieville, and Thibodaux, respectively.

The figures of length do not vary much when compared with those reported by Yarwood (235). He reported that an onion mildew strain in California had conidia which measured 18-29 x 40-72 u.

Since the figures of width seem to be different, the statistical analysis conducted shows that the coefficients of variation in width for the three locations are 11.76, 9.37, and 9.09. This indicates no doubt as to the validity of the test.

Data show that 26.0%, 27.3%, and 40.3% of the conidia had a greater range in width than that reported by Yarwood. Also, the minimum width was not below 22.2 u (Table VII). However, a large number of spores from each location were still within the limits of the measurements for the California strain.

When Saccardo (170) described Peronospora destructor under the name P. Schleideni, he gave the dimensions 22-26 u x 44-52 u for the conidia.

The settling of the point that different strains exist must await comparative cultural studies of various collections of onion downy mildew, as has been suggested by Yarwood (235).

Table VI. STATISTICAL ANALYSIS OF CONIDIAL MEASUREMENTS

Location	N	Width Range u	$\bar{x}$	s	C.V. %
Baton Rouge	200	22.2-33.3	$26.9 \pm .32$	3.16	11.76
Labadieville	300	22.2-33.3	$28.4 \pm .26$	2.66	9.37
Thibodaux	300	22.2-38.8	$27.8 \pm .25$	2.53	9.09

Table VII. DISTRIBUTION OF CONIDIA WITHIN THEIR WIDTH CLASSES

Location	N	% Conidia in the class					div.* u
		(6-6.5) 22-24	(7-7.5) 26-28	(8-8.5) 30-32	(9-9.5) 33-35	(10-10.5) 37-39	
Baton Rouge	200	30.5	43.5	23.0	3.0	0.0	
Labadieville	300	8.7	51.0	37.0	3.3	0.0	
Thibodaux	300	9.0	63.7	24.0	3.0	0.3	

\* One division equals 3.7 u.

#### D. Discussion and Literature Review

Yarwood (235) mentioned three methods of determining mildew incidence. These are:

1. microscopic observation of tissues for characteristic mycelium, haustoria, and oospores,
2. determination by the characteristic symptoms, and
3. determination by presence of conidiophores and conidia.

Microscopic observation of tissues is useful and essential in doubtful cases, but it is too laborious for most studies. The detection of the disease by symptoms is perhaps the most useful method of diagnosis, but is subject to error unless one is well acquainted with the disease. The occurrence of downy mildew conidiophores on the surface of living onion leaves is the most reliable index of downy mildew infection, but unfortunately sporulation does not occur with regularity under field conditions.

Classification of onion plants (foliage and scapes) for their reaction to mildew into susceptibles and resistants, as has been followed in this investigation, will throw much light on the nature of inheritance. Chester (31) indicated that when diseased plants or plant parts are total losses and not partial losses, or when all diseased plants or plant parts are partial losses to the same degree, counts of diseased plants or plant parts and conversion of the counts into percent gives accurate measures of disease intensity. Thus we find this method of scoring disease intensity most useful and reliable in dealing with:

- a. diseases in which the entire plant is rapidly killed, with few plants exhibiting partial loss;

- b. cases in which diseased plants, while not killed, are all injured to approximately the same extent;
- c. instances in which the percent of infected plants is well correlated with the degree of injury;
- d. diseases which cause total, not partial, destruction of the commercially valuable parts;
- e. diseases in which plants or organs, even if lightly infected, are total losses from the commercial standpoint; and
- f. cases in which diseased plants or tissues are so rare that differences in degree of infection have little statistical significance.

Downy mildew of onion is an example of cases a, c, and d combined.

In the long run control by resistant varieties is the best and cheapest method of disease control. In fact, there are many diseases that can be controlled in no other way.

The earliest attempts at producing disease-resistant varieties consisted of selecting resistant individuals from otherwise susceptible populations, multiplying these individuals, and continuing reselection until true-breeding resistant lines were obtained. Later and more effective efforts have been directed at deliberately producing resistant varieties by crossing resistant with susceptible parents, selecting from the hybrid generation, and backcrossing the selected individuals with the more desirable parent until desirable, homozygous, resistant lines have been secured (30).

Walker (214) mentioned that the major point of contact between plant pathology and genetics has to do with resistance of plants to pathogenic agencies and the mode of inheritance of resistance and pathogenicity.

The interaction of host and parasite makes up an extremely diverse set of phenomena. Pathogens relate themselves to their hosts in a variety of ways. The relation of a given pathogen to its natural host substrate in most cases follows a definite pattern. The relation of the same pathogen to a resistant variety of the host species is usually a fairly definite departure from the pattern with a susceptible variety. When this interrelation is understood, it has been shown in many cases to be a definite Mendelian character (214).

In 1900 there was the simultaneous discovery by three independent observers, De Vries, Correns, and Tschermak, of the work on inheritance carried out by Gregor Mendel and communicated to the Brun Society in 1865. Soon after this rediscovery Biffen (17) at Cambridge University showed that resistance to yellow rust (Puccinia glumarum) in wheat behaves as a simple Mendelian character. Because of the historical and scientific importance of Biffen's work it is summarized as follows:

On crossing immune and susceptible wheat varieties the  $F_1$  was susceptible. On selfing, these susceptible individuals produced immune and susceptible descendants in the proportion of one immune to three susceptible. The degree of susceptibility was variable. The relatively immune forms bred true to this characteristic in the succeeding generations (17).

It was found in some cases that resistance to disease was dominant over susceptibility. In others, it was found to be recessive. There are few examples which demonstrate the complex nature of disease-resistance inheritance, but the majority of reported cases indicate that resistance or susceptibility to a disease is simply inherited (i.e. one pair of genes governing the reaction).

The mode of inheritance of downy mildew on onion was only reported by Jones, Porter and Leach (100). Their data indicate that scape resistance was dominant over susceptibility. On the other hand, in the Calred-Red Creole hybrids scape resistance was a recessive character. This apparent discrepancy might be due to several causes. It could be attributed to the nature of the material studied, or to the existence of different strains of the pathogen, or to some other reason. Tins (199) tested the Red Creole, the Calred, and the first generation hybrids between the two varieties for reaction to mildew. The disease was rather severe.  $F_1$  was susceptible in foliage. Calred plants showed resistance.

Results obtained in the present studies, and conclusions reached that resistance to mildew in onion scapes is inherited as a recessive character governed by two duplicate genes have their similarities with resistance to some other plant diseases regardless of the nature of the causal organism (i.e. a bacteria, or a fungus, or a virus).

#### Complex inheritance of resistance to some diseases:

Several examples are cited here, including diseases of some field crops (e.g. maize, rice, oats, wheat) as well as diseases of some vegetable crops (e.g. beans, cowpeas, cucumber, peas, potato).

In maize, Wellhausen (220) found that at least three independently inherited dominant supplementary factors are involved in the inheritance of resistance to bacterial wilt (incited by Phytophthora stewarti). The three factors were designated  $Sw_1$ ,  $Sw_2$ , and  $Sw_3$ .

When all three factors are present in the dominant condition a high degree of resistance results. When none of the dominant factors is present a high degree of susceptibility results. The heterozygote  $Sw_1sw_1 Sw_2sw_2 Sw_3sw_3$  appears to be fully as resistant as the homozygote  $Sw_1Sw_1 Sw_2Sw_2 Sw_3Sw_3$ . These factors, when in combination, seem to act supplementary or additive.  $Sw_1$  combined with  $Sw_2$  results in a much higher degree of resistance than when either is present singly. The addition of the third factor  $Sw_3$  increases the resistance still further, although only slightly.

In rice (Oryza sativa L.), Adair (1) presented data on the inheritance of reaction to Helminthosporium oryzae and Cercospora oryzae. The results indicated that reaction to H. oryzae was controlled by several genetic factors and that, in the particular crosses studied, resistance was recessive. Supreme Blue Rose, a susceptible variety, has at least one factor for reaction to C. oryzae dominant to the factor for reaction to this fungus in the resistant varieties used. In crosses involving the susceptible varieties Zenith, Early Prolific, and Carolina Gold, the factor for susceptibility to C. oryzae was recessive.

Very recently, Welsh and Johnson (221) reported on the inheritance of reaction to 12 different races of stem rust of oats (incited by Puccinia graminis avenae). Their results indicate the existence of 2 genes governing resistance to all races in some of the crosses, with resistance being dominant.



Shobeski and Wu (175) found that the Perennial wheat, resulting from the cross Chinese x (Chinese x Agropyron elongatum), carries three complementary dominant genes for resistance in the seedling stage to some of the existing races of stem rust.

The inheritance of resistance to three physiologic forms of Colletotrichum lindemuthianum has been studied by Andrus and Wade (4) in intervarietal crosses of bean (Phaseolus vulgaris L.). Monohybrid and dihybrid ratios were obtained with all 3 forms of the pathogen, and trihybrid ratios also were obtained with 2 forms. A system of 10 genes in 3 allelomorphic series, involving both duplicate and complementary genes for resistance, 1 dominant gene for susceptibility, and gene interactions at 3 points, is proposed as the simplest Mendelian hypothesis that will coordinate all the data for 2 forms of the fungus.

Schuster (171) studied the mode of inheritance of halo blight (incited by Pseudomonas medicaginis var. phaseolicola) of bean. At least two dominant factors must be present for susceptibility to express itself in some crosses between resistant and susceptible varieties.

Fennel (61) made an interspecific hybrid between the cowpea (Vigna sinensis) and the yardlong bean (V. sesquipedalis) in an effort to control the powdery mildew of cowpeas (incited by Erysiphe polygoni). Resistance to this disease has segregated as a multiple factor recessive. Two or possibly three genes are involved.

Shifriss, Myers and Chapp (180) found that the genetical mechanism involved in the manifestation of virus symptoms in the cucumber follows a developmental pattern. At the cotyledon stage 3

complementary genes are responsible for the ability or the failure to produce chlorosis. As the  $F_2$  population reaches the true-leaf phase, the initial genetical ratio is constantly changing during development. At this phase several gene modifiers, in addition to the 3 basic genes, also play a role in the manifestation of virus symptoms.

Wark (218) found that resistance to Ascochyta pisi in garden peas is due to the presence of three Mendelian factors, all of which must be present for the manifestation of resistance. Resistance to this disease was found to be dominant.

In potato, Black (19) found that the inheritance of resistance to potato wart disease is dependent upon the cumulative interaction of three factors inducing resistance.

Very recently, Black (20) found that the resistance to Phytophthora infestans exhibited by Solanum demissum and seedlings bred from it is due primarily to the hypersensitive condition of the protoplasm. This condition is manifested in the presence of one or more major resistance genes, of which four have been identified, viz.  $R_1$ ,  $R_2$ ,  $R_3$ , and  $R_4$ . Each major gene confers resistance to the common strain and to a particular group of specialized strains of the parasite. The genes are inherited independently in simple Mendelian fashion. A series of minor genes, associated with morphological and physiological characters of the plant, modify the phenotypic expression of the major gene system, and so determine the degree of susceptibility phenotypes and the extent of necrosis in resistant ones.

Addendum:

Breeding work on onions looking toward varietal improvement and disease and insect resistance was initiated at the California Agricultural Experiment Station in 1922 by Dr. H. A. Jones (43, 94). The program of breeding is being conducted by the Federal Government and by the State-supported research institutions (86).

Almost thirteen years ago the United States Department of Agriculture entered into a cooperative agreement with several States, the broad aims of which included the development of onions more resistant to mildew, smut, purple blotch, thrips, pink-root and storage rots (141). In 1950 there were 18 states, namely, California, Colorado, Connecticut, Idaho, Illinois, Indiana, Iowa, Louisiana, Massachusetts, Michigan, Minnesota, Nebraska, New York, Ohio, Oregon, Texas, Utah, and Wisconsin cooperating with the Division of Vegetable Crops and Diseases, U.S.D.A. in the National Onion-Breeding Program (208).

This extensive cooperative program is under the leadership of Dr. H. A. Jones, to whom a volume of *Herbertia* (founded by the American Plant Life Society) had been dedicated in recognition of his outstanding work in onion breeding (2). Jones (87) in his autobiography says:

"My big fall and winter job was removing sprouted and rotted onions from the shallow storage trays. This seems somewhat significant now, but I am sure that as a young boy, sorting onions until my fingers were numb and my feet cold, I had no desire at all to become an onion fancier. My work on the development of hybrid onions has certainly been a most fascinating and satisfying undertaking. I am indeed glad that those numb fingers and cold feet in boyhood did not forever keep me away from onions."

Although disease resistance offers the most nearly ideal solution of the problem of disease prevention, two difficulties must be borne in mind. Disease resistance may comprise resistance only to one particular disease and only a specific variety may be resistant. In the second place the possible variations or mutations of the disease organism must be constantly kept in mind. An established or at least apparent resistance may be completely upset by such developments in the parasite. Resistance, therefore, must not only be established, but also be maintained (66).

Hasfield (79) stated that the future in plant breeding lies in the development of morphological and anatomical resistance to, and tolerance of, pathogenic organisms. In this way a uniform barrier of resistance to all physiologic races will be set up, thereby excluding the new biotypes which tend to nullify the results achieved by selection on a narrower basis.

## INHERITANCE OF SOLUBLE SOLIDS

### Experimental Methods

During the season of 1950-51, some hybrid populations were grown in the field and in the greenhouse from seed. They produced bulbs in the spring of 1951. These bulbs (a total of 705) were examined after being harvested, cured, and stored at 35° F. Material from the field was stored for 7 weeks, whereas that from the greenhouse was stored for 12 weeks in cold storage. Lots selected for this study were three  $F_2$  populations of the cross Red Creole x Calred varieties, and the two parental varieties. These populations were:

La 30	Calred		
La 30g	"		
La 32	Red Creole		
La 32g	"		
La 7	Red Creole (949) x Calred (946).	$F_2$ .	( $F_1$ #1703)
La 7g	"	"	"
La 13	"	"	$F_2$ . ( $F_1$ #1711)
La 13g	"	"	"
La 15	"	"	$F_2$ . ( $F_1$ #1714)
La 15g	"	"	"

All the lots referred to as (g) were grown in the greenhouse, and the rest were grown in the field (Mill Farm) at Baton Rouge, La.

Since the percentage of soluble solids varies in the different parts of an onion bulb, i.e. percent soluble solids increases from the outer to inner fleshy scales, and increases from the top to

base of the bulb, it was deemed necessary to take a representative sample of each bulb. The procedure followed consisted of the determination of the percent soluble solids in one-half or one-fourth of each bulb. The juice was extracted by means of a hydraulic press. Half of a bulb, or one-quarter in case of large bulbs, was placed in a Carver test cylinder (1-1/8" diameter) and by means of the Carver Press a pressure of 2,000 lbs. per square inch was applied. In the preparation of the sample for the press the dry scales were removed as well as the first outer fleshy scale. The stem plate was cut and also the extreme top (neck) of the bulb. The juice was collected by using a dropper, and the sample was placed on the prism of a hand-type Zeiss Abbe refractometer which has a reading accuracy of  $\pm 0.2\%$ . Data obtained by the use of the refractometer indicate the percentage of soluble solids in the juice.

Dry-weight determinations were made for about one-tenth of the total bulbs in the populations. The sample was dried in a ventilated oven at  $60^{\circ}$  C. for 48 hours. Bulbs used for dry-weight determinations were cut into quarters. One quarter was used for oven drying, another for refractometer reading. Both refractometer reading and dry-weight determination was performed soon after cutting the bulb.

#### Statistical methods used:

Correlation and regression coefficients for percent dry matter and percent soluble solids were calculated. To test the significance of the regression coefficient, the standard error of estimate (Se) and  $t$  values were obtained.

For determination of the heritability of the character, the components of variance method was used. The formula is:

$$\text{Heritability value (P}_2\text{)} = \frac{V_G}{V_G + V_E}$$

$$V_G \text{ (genetic variance)} = s^2 P_2 - V_E$$

$$V_E \text{ (environmental variance)} = \frac{s^2 P_1 + s^2 P_2}{2}$$

For estimation of the minimum number of genes responsible for the expression of a character a formula developed by Wright (231) was used. It is:

$$\text{Minimum number of genes} = \frac{D^2}{8 (s^2 P_2 - s^2 P_1)^*}$$

D = genetic range of the two parents.

\*  $s^2$  of Calred parent was used instead of  $P_1$ .

### Experimental Results

Data on the percentage of soluble solids of the two parents and the three  $F_2$  populations are presented in Table VIII. The frequency distribution of percent soluble solids in each  $F_2$  population, as shown in the frequency polygons (Fig. 1, 2, 3), was normal (or approximately so) and unimodal, indicating quantitative inheritance controlled by multiple genes.

The Red Greole parent is highly pungent. It showed 15.83% and 16.34% of soluble solids when grown in the field and in the greenhouse respectively. On the other hand, pungency of the Calred parent is low. It showed 5.42% and 6.62% of soluble solids when grown in the field and in the greenhouse respectively.

The average of solids percentages of the two parents grown in the field was 10.62%, but in any  $F_2$  population the mean of solids percentage was lower, i.e. 8.69%, 9.46%, 9.64%. This was interpreted to indicate partial dominance of the low-solids percentage over the high-solids percentage. The same general conclusion was drawn from the greenhouse data which indicate that the mean of the two parents was 11.43% and the means of  $F_2$  populations were 9.39%, 10.03%, and 11.11% (Tables IX, X). Additional evidence of the dominance of the low-solids percentage is that in each  $F_2$  population grown in the field, the number of bulbs having soluble solids percentage below the  $F_2$  mean exceeded the number of bulbs having soluble solids percentage above this mean (Table XI).



The coefficient of skewness was calculated by applying the formula

$$sk = \frac{\bar{x} - \text{mode}}{\text{standard dev.}}$$

It was found to be 1.00 and .40 for the  $F_2$  populations, La 13 and La 15, indicating a positive skewness.

Concerning the type of gene action, data are presented in Table XII. The agreement between the obtained means and those calculated on the assumption that the effects of the genes are geometrically cumulative was closer than was the agreement between the obtained means and those calculated on the assumption that the genes are arithmetically cumulative. Since all  $F_2$  populations were descended from the same parent plants (viz. Red Creole #949 and Calred #946) we may obtain the average of their means. This is found to be 9.26% and 10.15% for  $F_2$  populations grown in the field and in the greenhouse, respectively. In either case the average  $F_2$  mean was similar to, or slightly below the expected mean on the basis of geometric gene action. This suggests that genes governing the percentage of soluble solids probably act in a geometric manner in the material studied, with partial dominance of the low-solids percentage.

Variation in the Red Creole parent grown in the greenhouse or in the field was relatively great, partly because of its apparent heterozygosity. On the other hand, the Calred parent showed much less variation. Consequently, the Calred parent was used alone in the calculation of variation due to environment instead of using the average variance of the two parents. However, the effect of the environment might not be the same on low- and high-solids types. The

figures for heritability indicate that selection work for high-solids types or vice versa would be effective under greenhouse and field conditions where the heritability values were found to be from 71% to 73%, and from 76% to 81%, respectively.

Since the Red Creole variety was apparently not homozygous, the Red Creole parent plant used in this cross could have had a soluble solids percentage varying from 13% to 17%. This makes it impossible to determine with any degree of exactness the number of genes involved. However, the results suggest that four to ten pairs of genes may have been involved in the difference between the two parents.

The percentage of dry matter content and soluble solids percentage obtained from the same bulb samples are shown in Table XIII and presented graphically in Figure 4. A straight line regression was obtained. The  $r$  value was 0.87 and the value for the regression coefficient was 0.99. Both of these values were highly significant. It is concluded that the percentage of soluble solids as determined by the refractometer may be used as a method of estimating the approximate dry matter percentage. This confirms the work of Feskett and Peterson (65).

Fig. 1. Frequency distribution of Percent Soluble Solids in the  $F_2$  (La 7) and parents grown in the field.

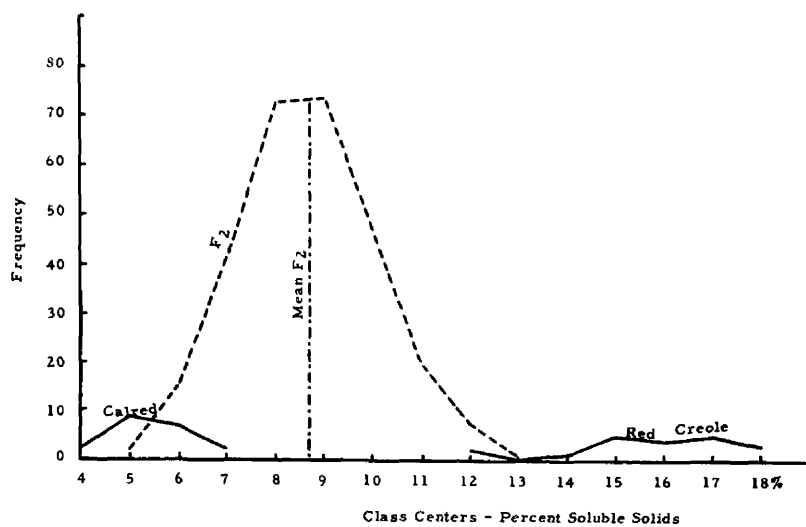


Fig. 2. Frequency distribution of Percent Soluble Solids in the  $F_2$  (La 13) and parents grown in the field.

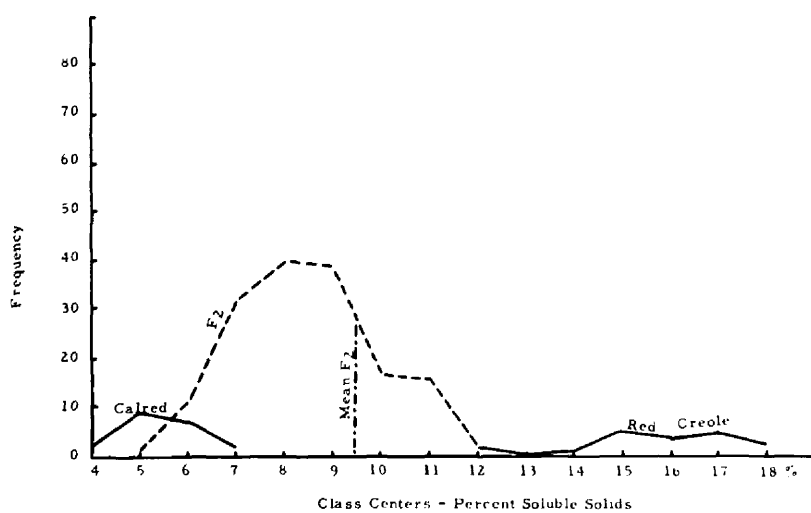


Fig. 3. Frequency distribution of Percent Soluble Solids in the  $F_2$  (La 15) and parents grown in the field.

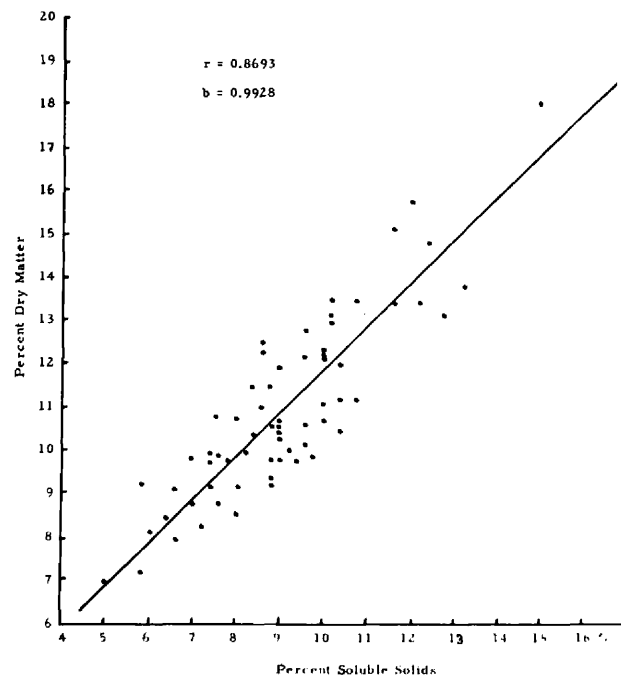
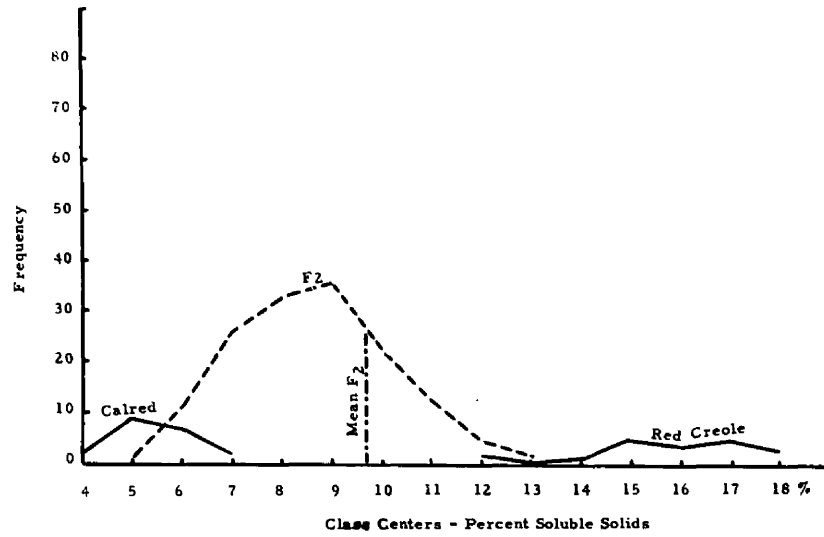


Fig. 4. Scatter diagram showing the regression of Percent Dry Matter on Percent Soluble Solids of varieties and hybrids.

Table VIII. FREQUENCY DISTRIBUTION FOR SOLUBLE SOLIDS PERCENTAGE IN A CROSS BETWEEN RED CREOLE x CALRED

		Class Centers, Percent																N	$\bar{x}$
		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18			
Material grown in the field	Red Creole (La 32)									2	0	1	5	4	5	3	20	15.53 $\pm$ 0.40	
	Calred (La. 30)	2	9	7	2												20	5.42 $\pm$ 0.05	
	F <sub>2</sub> (La 7)		2	13	41	73	74	46	20	8	1						278	8.69 $\pm$ 0.08	
	F <sub>2</sub> (La 13)		1	11	32	40	39	17	16	2	1						159	9.46 $\pm$ 0.11	
	F <sub>2</sub> (La 15)		1	11	26	33	36	23	13	5	2						150	9.64 $\pm$ 0.13	
Material grown in the greenhouse	Red Creole (La 32g)												3	2	3	2	10	16.34 $\pm$ 0.33	
	Calred (La 30g)			5	3	2											10	6.62 $\pm$ 0.08	
	F <sub>2</sub> (La 7g)				2	4	6	3	3	1	1						20	9.39 $\pm$ 0.33	
	F <sub>2</sub> (La 13g)					4	2	6	4	0	2						18	10.03 $\pm$ 0.36	
	F <sub>2</sub> (La 15g)					2	0	6	3	5	4						20	11.11 $\pm$ 0.34	

Table IX. SOLUBLE SOLIDS PERCENTAGE IN PARENTS AND  
THREE  $F_2$  POPULATIONS GROWN IN THE FIELD

Lot	Pedigree	Plants tested No.	Mean %	C.V. %	Heri- tability value %
La 7	(Red Creole x Calred) $F_2$	278	$8.69 \pm 0.08$	16.31	76
La 13	" "	159	$9.46 \pm 0.11$	15.38	77
La 15	" "	150	$9.64 \pm 0.13$	16.71	81
La 32	Red Creole	20	$15.83 \pm 0.40$	11.38	
La 30	Calred	20	$5.42 \pm 0.05$	4.04	

Table X. SOLUBLE SOLIDS PERCENTAGE IN PARENTS AND THREE  
 $F_2$  POPULATIONS GROWN IN THE GREENHOUSE

Lot	Pedigree	Plants tested No.	Mean %	C.V. %	Heri- tability value %
La 7g	(Red Creole x Calred) $F_2$	20	$9.39 \pm 0.33$	15.89	71
La 13g	" "	18	$10.03 \pm 0.36$	15.11	72
La 15g	" "	20	$11.11 \pm 0.34$	13.79	73
La 32g	Red Creole	10	$16.34 \pm 0.33$	6.32	
La 30g	Calred	10	$6.62 \pm 0.08$	3.82	

Table XI. DISTRIBUTION OF BULBS IN THEIR RESPECTIVE CLASSES OF SOLUBLE SOLIDS PERCENTAGE, IN  $F_2$  POPULATIONS

Lot	Mean %	Number of bulbs having a percentage of soluble solids			N
		close to $\bar{x}$	Above $\bar{x}$	Below $\bar{x}$	
La 7	8.69 $\pm$ 0.08	25	124	129	278
La 13	9.46 $\pm$ 0.11	20	65	74	159
La 15	9.64 $\pm$ 0.13	16	63	71	150

Table XII. OBTAINED AND THEORETICAL MEANS FOR SOLUBLE SOLIDS IN  $F_2$  POPULATIONS

Lot	Actual mean	Expected mean on the basis of:	
		Arith. gene action	Geometr. gene action
La 7	8.69	10.62	9.26
La 13	9.46	"	"
La 15	9.64	"	"
La 7g	9.39	11.48	10.40
La 13g	10.03	"	"
La 15g	11.11	"	"

Table XIII. PERCENTAGE OF SOLUBLE SOLIDS (REFRACTOMETER DETERMINATION)  
AND PERCENTAGE OF DRY MATTER (OVEN DETERMINATION)

Sample Lot and Bulb				Dry		Sample Lot and Bulb				Dry	
No.	No.			Solids	matter	No.	No.			Solids	matter
				%	%					%	%
1	La 32g	-	10	15.0	18.06	39	La 13	-	10	7.4	9.16
2	La 32	-	10	15.6	19.86	40	"		20	7.6	8.76
3	"		20	12.0	15.84	41	"		30	11.0	13.01
4	La 30g	-	10	5.8	9.23	42	"		40	9.8	9.94
5	La 30	-	10	5.0	6.96	43	"		50	10.4	11.98
6	"		20	5.8	7.22	44	"		60	8.6	11.00
7	La 7g	-	10	9.0	9.78	45	"		70	7.6	10.83
8	"		20	10.8	13.45	46	"		80	7.6	9.87
9	La 7	-	10	6.6	9.06	47	"		90	10.0	12.24
10	"		20	10.8	11.20	48	"		100	9.2	10.03
11	"		30	10.0	12.18	49	"		110	9.6	10.57
12	"		40	7.2	8.24	50	"		120	8.6	12.45
13	"		50	11.4	11.00	51	"		130	10.0	12.40
14	"		60	6.0	8.06	52	"		140	7.4	9.75
15	"		70	8.2	10.00	53	"		150	7.6	12.22
16	"		80	7.0	9.83	54	"		158	10.0	12.32
17	"		90	9.2	8.85	55	"		159	8.0	10.70
18	"		100	7.8	9.66	56	La 15g	-	10	11.6	13.40
19	"		110	9.0	10.50	57	"		20	12.2	13.44
20	"		120	9.0	10.72	58	La 15	-	10	10.0	11.81
21	"		130	8.8	9.33	59	"		20	12.4	14.79
22	"		140	10.4	10.45	60	"		30	8.8	9.82
23	"		150	8.0	8.53	61	"		40	8.8	9.28
24	"		160	8.6	12.31	62	"		50	10.0	11.79
25	"		170	8.8	10.58	63	"		60	10.0	10.67
26	"		180	7.4	9.93	64	"		70	9.6	10.12
27	"		190	9.4	9.80	65	"		80	6.6	7.95
28	"		200	7.8	9.68	66	"		90	9.6	12.77
29	"		210	9.0	10.40	67	"		100	9.0	11.86
30	"		220	7.0	8.77	68	"		110	11.6	15.17
31	"		230	10.0	11.13	69	"		120	8.4	11.54
32	"		240	9.0	9.68	70	"		130	10.2	13.09
33	"		250	9.0	10.32	71	"		140	10.2	12.99
34	"		260	8.8	11.67	72	"		150	10.2	13.52
35	"		270	9.6	12.20	73	"		160	13.2	13.84
36	"		277	6.4	8.43	74	"		170	8.4	10.34
37	La 13g	-	10	9.0	10.70	75	"		180	10.4	11.18
38	"		18	12.8	13.09	76	"		186	9.0	10.42



### Discussion and Literature Review

The particular constituent to which the onion owes its pungency was identified as a volatile oil, known chemically as allyl-propyl-disulfide ( $C_3H_5$ ) $_2$ S( $C_3H_7$ ). In 1934, Platenius and Knott (152) mentioned that the only measure of pungency available was the tasting test, which on the whole, is very inaccurate because of the accumulative effect of successive tastings. A more satisfactory measure of pungency in onions became available through the development of a chemical method which made it possible to express the results in definite numerical values. This method is based on the quantitative determination of sulfur in the volatile onion oil after the latter has been isolated by means of steam distillation. The Red Greco variety was found to be the most pungent type of the varieties tested.

Since this chemical method, as described in detail by Platenius (150), involves steam distillation it is time-consuming and cannot be recommended as routine procedure when a large number of samples is involved.

A Russian investigator (Biryukov) has shown that the refractive index of onion pulp is related to dry-matter content. Calculation from his tabular data, made by Mann and Hoyle (122), showed a high positive correlation between dry-weights (oven) and refractometer readings ( $r = 0.96$ ).

The mode of inheritance of onion pungency has not been reported before. However, the extensive work carried out by Platenius and Knott (153) was concerned with the pungency of onions as affected

by inherited characteristics, growing temperature, soil type, water supply, and storage. Of the different factors studied, the inherent characteristics of the varieties examined had the most pronounced influence on pungency, when the relative pungency of the different samples of onions was measured by determining the volatile-sulfur content of the bulbs. Since these differences were smaller on the dry weight basis, it seems that, to some extent, relative pungency is a question of concentration of dry matter. Jones and Bisson (90) drew the following conclusion:

"Evidently, those varieties that are considered mild and of rather poor storage quality have the highest moisture content, whereas those that are the most pungent and keep best in storage have the lowest moisture content."

According to Jones and Bisson (90) the Red Creole variety had 15.87% dry matter. This determination agrees very closely with the percentage of soluble solids found in the present studies for this variety. There is no available report on the percent solids or dry matter of the Calred variety. However, it has been described as having a mild flavor (98). One of the parents of the Calred variety is the male-sterile Italian Red 13-53. According to Mann and Hoyle (122) this strain had 7.62% dry matter, and the refractometer reading of the juice of the two outer scales was 5.63%. Bulbs of Lord Howe Island—the male parent of the Calred variety—were reported to be very mild-flavored (154).

Consequently, the difference in the degree of pungency between the two varieties that constitute the parents of the cross investigated is great and would permit feasible genetic interpretations.

Zeller (238) found that the concentration of sugars, which constitute much of the dry matter of the onions, increases from the outside toward the center of the bulb and from the top toward the base. Mann and Noyle (122) found that the percent dry-weight increases from the outer to the inner scales. Very recently, Kehr and Tims (105) reported that soluble solids in the Creole variety over a four-year period have averaged 16.04%. Their results indicate that soluble solids in the Creole onion increase from the outside to the inside and from the top to the bottom of the bulb. Refractometer readings showed that the bottom half of the bulb exceeds that of the top half by 16.36% and that the growing point exceeds that of the outer scale by 65.40%. The specific gravity method was used to determine soluble solids in the Creole. Results indicated a correlation coefficient of .884 between solids and specific gravity readings. This compares very favorably with the correlation between solids and refractometer readings which gave a correlation of .855 in 258 comparisons, indicating that the specific gravity method is equal in accuracy to the refractometer method (105).

The type of soil on which the onions are grown is another important factor that determines pungency (153). Onions grown under conditions of high moisture supply showed a small but consistently lower content of volatile sulfur, according to Flatenius and Knott (153). On the other hand, data presented by MacGillivray (119) indicate that irrigation increased the total amount of volatile sulfur produced per acre, but did not greatly affect the percentage composition of the onions as to pungency.

Lorenz and Hoyle (118) studied the effect of curing and time of topping on percentage dry matter. Bulbs with tops intact were much higher in percentage dry matter after curing than bulbs with the tops cut off. The differences might be due to (a) greater loss of water from intact bulbs due to withdrawal by tops or (b) movement of solid materials from the tops to the bulbs during the curing period. Data indicate that both factors operate, but apparently the second factor is the more important.

It is concluded from data obtained in the present studies that the inheritance of soluble solids percentage in the onion is similar to that of a quantitative character, and is differentiated by the interaction of genes in a geometric fashion.

At least two numerical systems are related to the nature of the interactions of the genes differentiating quantitative characters, these interactions being determined by the measurement of end products.

1. There may be no interactions between the genes affecting the quantitative character. Then, the effects of these genes will be arithmetically cumulative.
2. The nature of the interactions of the genes affecting the quantitative character may be such that the effects of the genes are geometrically cumulative. (155)

Powers (155) pointed out that more than one type of interaction of the genes differentiating quantitative characters must exist when measurements of end products are involved. He found that small size of tomato fruit is partially dominant, and the effects of genes are geometrically cumulative.

A brief explanation of arithmetic and geometric actions of genes is given by Smith (183).

**Arithmetic action:** Each gene substitution adds or subtracts its contribution to that of the residual genotype. If the absolute amount added to the phenotype is the same regardless of the other genes present the gene in question would be considered as having independent arithmetic action.

**Geometric action:** Each gene substitution multiplies or divides the residual genotypic value by a certain amount. The absolute phenotypic contribution of the gene would vary according to the magnitude of the residual genotype, but if it acts as a fixed multiplier the gene would be considered independent and geometric in action (183).

The multiple-factor theory of the inheritance of quantitative traits postulates the operation of many genes in determining a given character. It seems usually to have been assumed that each gene produces a constant and specific effect on the phenotype and that these effects are arithmetically cumulative, so that a segregating  $F_2$  population should show a symmetrical distribution (182).

Ragnussen (161) presented evidence that multiple genes interact in such a way that their individual expression may be greatly modified. The visible effect of a certain factor is held to be smaller the greater the number of factors acting in the same direction. Genes affecting quantitative traits should thus be geometrically rather than arithmetically cumulative.

In this connection, Sinnott (132) assumed that the effect of a given gene increases in proportion to the effectiveness of the rest of the genotype. A gene may thus be thought of as adding a definite percentage to what the rest of the genotype produces, rather than a definite absolute value.

Sinnott also mentioned that the character of the genic effect can best be determined from a study of the distribution of an  $F_2$  population as to a given quantitative trait. If this is symmetrical about its mean, one must conclude that each gene makes a constant absolute contribution to the phenotype and that these are arithmetically cumulative. If the distribution is consistently asymmetric or skewed, however, this may be considered as evidence that the genes are interacting and producing a geometric or multiplicative effect (132).

Pearson and Bennett in their text (146) stated:

"Skewness is a characteristic of the frequency distribution. Standard deviation, for example, is a measure of the amount of dispersion. Skewness describes the nature of this dispersion. Symmetrical distributions are not skewed. In asymmetrical or skewed distributions, the number of observations either side of the mode is unbalanced."

In the positive skewness observed in the frequency polygons of the soluble solids percentage, the scores tend to cluster around the lower end of the distribution, and this may indicate an expression of dominance of certain of the segregating genes. These genes, in this case, were those which govern the expression of low-solids percentage.

The shape of the frequency distribution curve (graph) has been used by some as a basis for interpreting their results on quantitative inheritance. Smith (153) said that caution should be exercised, however, in interpreting skewness, for different causes, equally likely a priori and difficult to distinguish, may produce skewness in either direction.

Skewness in the frequency distribution of measurements of quantity may be due to dominance, the nature of gene action, physiological limits to phenotypic expression, interactions of various sorts, and metrical bias. It is difficult to distinguish between these different causes so that caution should be exercised in interpreting the genetic meaning of departures from a normal distribution curve (153).

The approximate minimum number of genes that interact to produce the expression of percent solids, was concluded to be around 4 to 10 pairs, according to Wright's formula. However, this formula is used for genes having equal effect and no dominance or epistasis. Wright (231) stated that any degree of dominance or of epistasis increases the estimate.

Smith (153) in his review on inheritance of quantitative characters, mentioned that the principle of multiple genic control is generally accepted in genetic explanations of quantitative inheritance, yet some characteristics involving hereditary differences in quantity are apparently determined by relatively few genes, and others, as plant height in maize, may be either multiple or monogenic in their inheritance.

In a species with a low chromosome number (in Allium Cepa  $2n = 16$ ) and presumably relatively fewer genes, some quantitative characters might be expected to be relatively simple in their inheritance. Smith also stated:

"The suggestion that hereditary factors controlling size, growth or quantity may have geometric, multiplicative, percentage or exponential effects is not a new idea; it can be found in earlier publications, notably those of Galton (1879), East (1913), Groth (1914), Zeleny (1920), and Wright (1922)."

The ultimate physiological or physico-chemical basis for inheritance of any quantitative character is unknown, but clues are suggested by certain results demonstrating inherited differences in the production of growth-regulatory substances, in the utilization of plant nutrition, and in the ability to synthesize materials vital to the life processes (183).

According to Bennett (14), a consideration of seasonal trends of some of the constituents of the Ebenezer onion indicates that the normal growth cycle may be divided into two parts. The first, consisting of about two-thirds of the total growing period, is spent in developing a top of great synthesizing powers, and is marked in the latter stages by a rapid gain in dry weight and a softening of the neck or shank of the plant. The second period is characterized by a gradual suspension of photosynthetic activity and by a more or less complete removal of solutes to the bulb. As a result of these physiological processes it may be generally stated that in the tops the content of the total ash and of all the nitrogen fractions, determined quantitatively, decreased with maturity accompanied by an increase of soluble sugars until signs of maturity developed; in the bulbs the content of all constituents increased.



Stephenson (157) believed that flavor formation in onion is an enzyme reaction. All evidence indicates that the enzyme and precursor cells are separate in the onion bulb. Flavor can be obtained only after the connecting cell walls have been ruptured under favorable pH and temperature conditions. When an onion is sliced, there is a rupturing of cells only at the cut surface. The lachrymator and sulfur-bearing flavoring compounds, in addition to such products as propyl alcohol and propionaldehyde, are formed by the cleavage of the precursor by the enzyme.

Addendum:

A long time ago Shakespeare (A Midsummer Night's Dream) said:

"If the boy have not a woman's gift  
To rain a shower of commanded tears  
An onion will do well."

Work in his text (225) introduced the chapter on onion by saying:

"The onion tells its own story, with pungent tang when eaten raw and with a characteristic milder flavor when cooked. It is laughed about and even ridiculed, but people like it though it brings unwanted tears and though the flavor sometimes lingers after appreciation has departed."

## INHERITANCE OF PIGMENTS

### A. Albinism in Seedlings

#### Experimental Methods

Data on albinism were taken for two series of observations. Data for the first series (Series A) were recorded in September, 1949. Total seedlings examined were 8,723. Data for the second series (Series B) were recorded in September, 1950. Total seedlings examined in this last series were 7,224.

Seedlings examined were of Red Creole, Calred,  $F_2$  and first back-cross populations. Seeds were planted in sterilized soil in small pots. Germination started after a few days and continued for about 10 to 12 days. Seedlings were counted shortly after passing the "knee" stage, when the tip of the cotyledon is withdrawn from the seed and above the soil, and the cotyledon straightens except for a slight kink which remains at the original locus of the knee. In some cases, when the soil is not too firmly packed, the seed may be lifted above the soil by the tip of the cotyledon (Plate IX).

In each population (a total of 35 lots were examined) the percentage of germination (normal + albino) and percentage of albinos were recorded. The chi-square test was used for determining goodness of fit of observed data to the Mendelian ratio 3:1.

In populations in which segregation occurred for albinism, the degree of association between percentage germination and percentage of albinos was measured by calculating the correlation coefficient ( $r$ ).

### Experimental Results

Albino seedlings were almost white, germinated normally, and continued growth for several days. Only a few remained alive after the first foliage leaf emerged from the longitudinal slit in the cotyledon, but without developing any green color. In general, albino seedlings perished before the end of the third week after germination had started.

Data on the occurrence of albinism in the different populations tested are presented in Tables XIV and XV. In the cross 950 x 945, five  $F_2$  populations (out of a total of six) produced albino seedlings. In four of these populations, segregation appeared to fit a ratio of 3 normal to 1 albino. In the reciprocal cross 949 x 946, six  $F_2$  populations (out of a total of nineteen) exhibited albinism. Five of these populations segregated into ratios which were a good fit to 3 normal to 1 albino.

These data indicate that albinism is inherited as a monogenic recessive character. The recessive gene, tentatively designated a, is lethal when it is present in the homozygous condition. Any  $F_2$  population producing albinos was the result of selfing a heterozygous  $F_1$  plant with the genetic constitution Aa. Due to the fact that some  $F_2$  progenies of a given cross exhibited albinism, but not all the progenies of that specific cross, it is concluded that one of the parents carried the heterozygous factor pair A-a.

The very low percentage of albinos found in both parents and the much lower percentage found in the first backcross populations may be

attributed to mutation of the gene A for green or normal color. If the gene A mutates to a recessive allele a, the seedling is albinotic, virtually without any chlorophyll. Unable to carry on photosynthesis, it soon dies.

The correlation between percentage of germination and percentage of albinos, in populations in which albinism was expressed, was positive but non significant. The r value was found to be .0025, indicating no relationship whatever between the incidence of albinism and percentage germination in a population of which some individuals carry the albino gene, a.

Table XIV. OCCURRENCE OF ALBINISM IN ONION VARIETIES, AND  
F<sub>2</sub> POPULATIONS. SERIES (A)

Lot	Pedigree		Number of seedlings			% Albino seedlings	Chi-square	P
			Normal	Albino	Total			
Calred x Red Creeole								
100	944	945	1166	0	1166	0.0		
101	"	"	878	0	878	0.0		
102	946	945	419	0	419	0.0		
103	"	"	324	0	324	0.0		
108	950	945	388	163	551	29.6	6.17	.01-.02
109	"	"	934	239	1173	20.4	3.38	<.01
110	"	"	447	151	598	25.2	.02	.80-.90
111	"	"	493	143	636	22.5	2.15	.10-.20
112	"	"	147	0	147	0.0		
113	"	"	434	120	554	21.7	3.29	.05-.10
Red Creeole x Calred								
104	949	946	410	99	509	19.4	8.36	<.01
105	"	"	343	107	450	23.8	.36	.50-.70
106	"	"	507	0	507	0.0		
107	"	"	384	0	384	0.0		
Calred*			114	5	119	4.2		
Red Creeole*			308	0	308	0.0		

\* progeny of non-selfed plants

Table XV. OCCURRENCE OF ALBINISM IN ONION VARIETIES,  $F_2$  AND FIRST BACKCROSS POPULATIONS. SERIES (B)

Lot	Pedigree	Number of seedlings			% Albino seedlings	Chi-square	P
		Normal	Albino	Total			
Red Creole x Galred							
La 1	949	946	265	0	265	0.0	
La 2	"	"	388	0	388	0.0	
La 3	"	"	350	0	350	0.0	
La 4	"	"	353	0	353	0.0	
La 5	"	"	328	0	328	0.0	
La 6	"	"	346	0	346	0.0	
La 7	"	"	420	0	420	0.0	
La 8	"	"	285	98	383	25.6	.07
La 9	"	"	324	116	440	26.4	.44
La 10	"	"	351	0	351	0.0	
La 11	"	"	273	76	349	21.8	1.93
La 12	"	"	283	0	283	0.0	
La 13	"	"	317	85	402	21.1	3.19
La 14	"	"	404	0	404	0.0	
La 15	"	"	336	0	336	0.0	
La 16	F <sub>1</sub> x Red Creole		229	1	230	0.4	
La 17	F <sub>1</sub> x Red Creole		270	3	273	1.1	
Galred*			781	28	809	3.5	
Red Creole*			493	21	514	4.1	

\* progeny of non-selfed plants

### Discussion and Literature Review

According to De Hann (45), the plants deficient in chlorophyll can be classified into unicolored ones (albina, xantha, chlorina, etc.) and variegated ones (spotted, striped, albomarginata, etc.). Albina plants are white and cannot assimilate: they die off as soon as the reserve food in the seeds has been used up. Xantha plants are yellow and died off as seedlings. The chlorina forms are distinguished from the normal green (typica) forms by decrease of all chlorophyll components. They reach the full-grown stage.

Rasmussen (160) was the first to report four types of chlorophyll deficiencies in the onion, in 1920. He found albina (weiss), xantha (gelb), chlorina, and T-chlorina. The albina and xantha died in the seedling stage. The chlorina were of yellowish-green color and mostly survived. The T-chlorina were paler in color than the chlorina and there was almost no survival. In one case he found a progeny of a plant which consisted of 52 green and 2 albino. This did not fit a 3:1 ratio, but he obtained this ratio, but he obtained this ratio in cases which involved green and xantha, green and chlorina, and green and T-chlorina. Green:chlorina:white occurred in the ratio of 9:3:4 as did green:chlorina:xantha.

Porter, Jones and Davis (154) were apparently the first to obtain the ratio of 3 normal to 1 albino in onion. They mentioned that the selfed progeny of an onion plant of Stockton G36 segregated for green and albino seedlings in the ratio of 3 green to 1 albino.



Jones, Clarke and Stevenson (92) mentioned that albino seedlings frequently occur in certain strains of the onion. They stated that albinism is inherited as a monogenic recessive a. Three other seedling characters, namely, yellow lethal, pale green lethal, and virescent (i.e. light green during the early stages of development and darker afterwards) seedlings were also studied. Each type was inherited as a monogenic recessive.

The present investigation on albinism has lead to the same conclusion drawn by Jones, Clarke and Stevenson (92). However, the hybrid material from which their conclusions were reached was not disclosed.

Albino seedlings which do not conform to Mendelian ratios have not been reported before in onion hybrids. However, the occurrence of such seedlings was reported in other cases, as in red clover (223). Apparently these seedlings are produced as mutations or resulted from chromosome aberrations that gave aberrant ratios.

De Hann (48) listed the following genera in which albino seedlings were reported:

Allium, Antirrhinum, Avena, Brassica, Delphinum, Dianthus, Festuca, Hordeum, Impatiens, Melandrium, Oryza, Pharbitis, Phaseolus, Phleum, Pisum, Ricinus, Secale, Sorghum, Senecio, Trifolium, Triticum, Urtica, Vicia faba, and Zea mays.

In red clover (Trifolium pratense L.), Williams (223) reported 8 simple recessive chlorophyll-deficient factors governing the formation of albino seedlings. At least six of these factors are genetically different.

Data presented by Shifriss (179) for the incidence of albino seedlings in two species of *Cucumis* and one species of *Citrullus*, suggest that albinism may be inherited as a recessive character whose expression is due to the presence of a lethal gene.

There are many recessive heritable chlorophyll abnormalities in maize. Many factors have been located in the genetic linkage map, and it is evident that there are several factors in each chromosome that in their interaction are responsible for the development of chlorophyll. These recessives are of two types, those that appear in seedling progenies and those that appear in mature plants. In a few cases, the same factor modifies chlorophyll development in both seedlings and mature plants (72).

The seedling types (in maize) are frequently lethal. They include 3 or more white-seedling types, each the result of a single gene in the homozygous recessive condition and 2 cases in which duplicate genes are involved (49).

Randolph (158) studied white seedlings of maize cytologically. He found plastid primordia present in all cells which normally would be green. Randolph concluded that in the case of white seedlings failure of the plant to become green is not to be explained as the result of an absence of plastids or plastid primordia. Later, Zirkle (239) found that the plastids in the albino seedlings were not due merely to their failure to complete development, but has an additional cause in a degeneration which ensues after they reach certain developmental stages. Except for the absence of pigments, the plastids appear entirely normal in the very young seedlings, and some leucoplasts actually mature in the epicotyl.

If it is assumed that Zirkle's findings are true in the case of the onion, then the gene a actually inhibits the formation of chlorophyll.

In a very recent review of the chloroplast, Weier and Stocking (219) classified the studies on chlorophyll inheritance into four groups:

(a) Chlorophyll and chloroplast characters are under complete control of the nucleus. Inheritance is strictly Mendelian. The nuclear gene involved may be stable or unstable.

(b) Plastid characters may be under nuclear control to the extent that the change in the plastid character is induced by a nuclear gene mutation. The changed plastid is thereafter inherited, independent of nuclear control.

(c) The chlorophyll character may result from an interaction between the plastids, nucleus, and other protoplasmic constituents. In this case the plastids are a distinct cooperating system in the inheritance mechanism.

(d) The plastid is an autonomous genetical unit, similar to the chromosome, in that it contains a gene, which is a self-duplicating unit, which may mutate, which is not controlled by the nucleus or cytoplasm, and which segregates at random during embryogeny and leaf histogenesis.

Weier and Stocking mentioned that groups a, b, and c are supported by a large body of excellent breeding work. The group d type of inheritance is less well documented and may be extremely speculative, involving plastogenes, viruses, chondriogenes, and random assortment of chloroplasts.

#### Addendum:

Speehr (186) successfully demonstrated that albino maize plants can be kept alive for several months by artificial organic nutrition with sucrose. These plants showed a definite increase in dry weight

above that of the seeds from which they sprang. They produced the same number of leaves as normal green plants and also staminate and pistillate inflorescences.

Of the hundreds of seedlings which were grown in the course of three years under a variety of conditions of light, temperature, and mineral nutrients, no tendency of the pure white seedlings to form chlorophyll was ever observed.

Spehr quoted Lebedeff who made comparative studies of various functions of green and albino maize plants, including rate of phototropic response, rate of growth, swelling of the seeds, rate of respiration, and metabolism of nitrogen compounds. Lebedeff concluded that the two forms of leaves did not differ in their assimilating mechanism but only in their capacity to utilize radiant energy.

## B. Bulb Color

### Experimental Methods

Three separate studies were made. In the first series, fourteen  $F_2$  populations from different crosses were grown from seed planted in September, 1949 at Baton Rouge, La. The plants were approaching maturity, about 7 months old, when the color data were obtained in 1950. The degree or the shade of red coloring was recorded according to a color photograph (Plate X) which showed the following red-color classes:

- I. Light Red
- II, III. Intermediate Red (III being darker than II)
- IV. Dark Red

In the second series, the same populations were examined. They were grown from seeds at Greeley, Colorado. The color reading was obtained on mature bulbs harvested when they were about 5 months old, in 1950. A color photograph (Plate XI) with approximately the same shade of red coloring as in Plate X, was used.

In the third series, the Photoelectric Reflection Meter with a green filter was used to record the color of mature bulbs of material grown at Baton Rouge in the season of 1950-51. This material consisted of Red Creole, Calred, three  $F_2$  and one first backcross populations. After being harvested and cured, they were stored at 35° F. for a few months until examination in October 1951. The color-recording instrument gave values of 5 units for the darkest red-color bulb ever found in the material, and 39 units for the lightest red-color bulb.

Total number of bulbs examined was 5,219, 1,728 and 760 in the first, second, and third series, respectively.

### Experimental Results

Clarke, Jones and Little (36) suggested that three pairs of genes, viz. C-c, R-r, I-i are involved in the development of any pigment in the onion. Red varieties carry the genes iCR. This theory is referred to in detail later. Data of the first and second series of studies are presented in Table XVI, and of the third series in Tables XVII and XVIII.

Data in general indicate the existence of a few modifying genes that seem to determine the red color in addition to the three major genes reported by Clarke, Jones and Little. It is thought that the number of modifiers may be 2 to 4. The number 4 is based chiefly on the existence of a 255:1 ratio in  $F_2$  populations. These modifiers are tentatively designated  $M_1, M_2, M_3$ , and  $M_4$  and are dominant over their alleles  $m_1, m_2, m_3$ , and  $m_4$ . The degree of red color is determined by the number of dominant modifiers present. In plants with more such genes, the color becomes darker.

Parents used in the crosses are of red color. One (viz. Calred) is dark red, and the other (viz. Red Creole) is light red. Consequently both parents should possess iCR genes, and furthermore the Red Creole should possess fewer dominant modifying genes than the Calred.

From general field observations the Red Creole variety shows a considerable degree of variation in color, but the bulbs used as parents were probably of the class "light-red". On the other hand, Calred bulbs were consistently of the class "dark-red" and just a few bulbs were of class III (intermediate dark red). The red-color

modifying genes present in the Calred, in a dominant condition, tend to give this variety the dark red color. Both Calred and Red Creole varied in the number of dominant modifiers present. Modifiers in the Red Creole are relatively few and are variable in number. Their existence in a heterozygous condition gives rise to the variation in color characteristic of this variety at present. Such a variation ranges from light-red to intermediate-red.

The two parents differed in the intensity of red color. Crosses between them showed red-color segregation in  $F_2$  and first back-cross populations. Regardless of the ratios suggested to exist in the different  $F_2$  populations, it is evident that in some of these populations the frequency of recovery of class I bulbs is very low (Table XVI). For example, in lot 100 only four bulbs (out of a total of 910) were of light-red color. In lot 101, there were only three, out of a total of 678 bulbs, of light-red color. Lots 110 and 113 behaved in a very similar manner.

It is noticed that more plants occurred in the dark-red class than in any other class. There is a tendency for the modifiers to be at least partially dominant for the intense red color, because of the predominance of the dark-red class.

Results indicate that Calred may possibly vary. The R gene gives us the red color in the presence of i and C genes. When dominant modifiers are present, the larger their number the darker becomes the color.



Within the cross 946 x 945, some  $F_2$  populations (e.g. lot 102) had a higher frequency of light-red bulbs than others (e.g. lot 103). This was also true with  $F_2$  populations from the cross 950 x 945, and from the reciprocal cross 949 x 946. These results indicate that one of the parents (or both), possibly the Red Creole, was heterozygous for a part of the modifiers involved. Data suggest that the number of the modifiers involved in the material studied was two as a minimum to as many as four.

Bulbs of the  $F_1$  generation grown in the greenhouses of Dr. Jones at Beltsville, Md. were observed. These bulbs were of dark-red color, and a relatively small number were found of the Class III (intermediate dark red). Throughout the present investigation no white bulbs were found in the segregating generations.

It is believed that data of the third series, in which the degree of red color was measured by the Photoelectric Reflection Meter, have thrown much light on the inheritance of red color of onion bulbs in general and the presence of red-color modifying genes in particular.

When the observations have been classified (Table XVII), and a graph was constructed for each  $F_2$  population, there was a skewed curve (Fig. 5), indicating that the red color of onion bulbs behaved as a qualitatively-inherited character. Bulbs of the dark-red class occurred more frequently than those of any other class. This would indicate a dominance of the dark-red color over the light-red color.

All Calred bulbs fell into one class, i.e. dark-red (5-9 units). Red Creole bulbs fell into the 20-24 units' class and higher. If we assume that classes of the range 20 to 39 units represent the

light-red color, and classes below 20 units (i.e. 5-19 units) represent dark-red color, one  $F_2$  population gave a ratio of 15 dark-red to 1 light-red and a second gave a ratio of 63:1 with dark-red color dominant (Table XVIII). It was concluded that dark-red color of onion bulbs was dominant over light-red color, and there were 2 or 3 pairs of genes acting as modifiers for the red-color intensity. Data of the first backcross also supported this conclusion. Here, a ratio of 3 dark-red to 1 light-red was obtained. This was an indication of the presence of two factor pairs difference. The chi-square test was used for determining goodness of fit of observed data to conventional Mendelian ratios.

The color units themselves may be used for drawing some conclusions. Red Creole bulbs had a mean of 28.1 units (i.e. light-red). Calred bulbs had a mean of 7.1 units (i.e. dark-red). The average of the two parents was 17.6 units. The mean of the three  $F_2$  populations was 8.3, 9.3, and 10.2 units. It is evident that the mean of any  $F_2$  population was distinctly below the average of the two parents. This would indicate a dominance of the small color-units over the high color-units, that is, a dominance of the dark-red color over the light-red color.

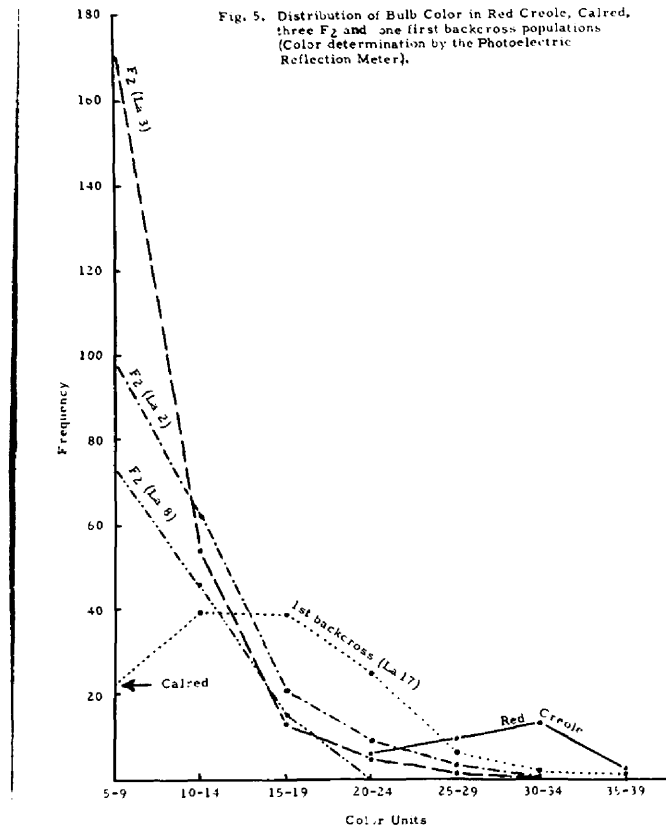


Table XVI. RECORD OF BULB COLOR IN F<sub>2</sub> POPULATIONS GROWN AT  
BATON ROUGE, LA. AND AT GREELEY, COLO. (G-LOTS) -  
1950

Lot	Distribution with- in color class:						N	Ratio II, III, IV: I	P
	I	II	III	IV					
Calred x Red Greele									
100	944	945	4	24	89	793	910	255:1	.80-.90
100-0	"	"	1	10	68	144	223	255:1	.80-.90
101	"	"	3	22	92	561	678	255:1	.80-.90
101-0	"	"	0	20	61	81	162		
102	946	945	12	23	79	125	239	15:1	.30-.50
102-0	"	"	2	8	44	47	101	15:1	.05-.10
103	"	"	5	13	82	123	223	63:1	.30-.50
103-0	"	"	0	6	18	13	37		
108	950	945	15	35	51	185	286	15:1	.30-.50
108-0	"	"	10	34	87	71	202	15:1	.30-.50
109	"	"	9	43	198	372	622	63:1	.80-.90
109-0	"	"	0	9	73	203	285		
110	"	"	2	20	84	219	325	255:1	.50-.70
110-0	"	"	0	3	36	80	119		
111	"	"	20	45	98	218	381	15:1	.30-.50
111-0	"	"	0	0	11	56	67		
112	"	"	2	18	28	57	105	63:1	.70-.80
112-0	"	"	0	1	11	21	33		
113	"	"	1	26	96	222	345	255:1	.70-.80
113-0	"	"	0	2	42	74	118		
Red Greele x Calred									
104	949	946	18	51	115	109	293	15:1	.90-.95
104-0	"	"	1	3	21	37	62	15:1	.10-.20
105	"	"	13	31	106	82	232	15:1	.50-.70
105-0	"	"	2	21	33	29	85	15:1	.10-.20
106	"	"	5	49	131	147	332	63:1	.90-.95
106-0	"	"	2	15	71	74	162	63:1	.70-.80
107	"	"	20	77	81	60	238	15:1	.10-.20
107-0	"	"	1	1	17	53	72	15:1	.05-.10

\* Class I-light red. II, III-intermediate. IV-dark red

Table XVII. FREQUENCY DISTRIBUTION FOR COLOR-SHADE UNITS IN CROSSES BETWEEN THE RED GREELE AND CALRED VARIETIES. DETERMINATIONS MADE BY THE PHOTOELECTRIC REFLECTION METER

Population	Class centers (units)							n	$\bar{x}$	s
	5-9	10-14	15-19	20-24	25-29	30-34	35-39			
Red Greele				6	9	13	2	30	$28.1 \pm .72$	3.968
Calred	22							22	$7.1 \pm .26$	1.230
$F_2$ (La 2)	99	62	21	9	3			194	$10.2 \pm .34$	4.786
$F_2$ (La 3)	173	54	13	5	1			246	$8.3 \pm .24$	3.843
$F_2$ (La 8)	74	46	15					135	$9.3 \pm .30$	3.461
First Backcross (La 16)	22	39	39	25	6	1	1	133	$15.2 \pm .51$	5.881

Table XVIII. BULB COLOR IN THREE  $F_2$  AND ONE FIRST BACKCROSS POPULATIONS, AS DETERMINED BY PHOTOELECTRIC REFLECTION METER.

		Distribution within color class:				
Lot		5-19*	20-39*	N	Ratio	P
	Red Creole x Calred					
La 2	949      946	182	12	194	15:1	.95-.98
La 3	"      "	240	6	246	63:1	.20-.30
La 6	"      "	135	0	135		
La 16	F <sub>1</sub> x Red Creole	100	33	133	3:1	.95-.98

\* 5-19 units class is dark red.  
 20-39 " " " light red.

### Discussion and Literature Review

In the onion the color of the bulb ranges from white to dark red and dark yellow, a great assortment of shades of red and yellow being known.

In 1931, Rieman (165) found five different genes governing bulb pigmentation in the onion: I-gene for incomplete inhibition of color, i-gene allowing expression of color, W-gene for red pigment,  $W^Y$ -gene for yellow pigment, w-gene for white. The gene for red W is dominant to the gene for yellow  $W^Y$ , and the gene for white w. He postulated a series of multiple alleles, namely, W,  $W^Y$ , and w.

In 1944, Clarke, Jones and Little (36) introduced a modification of Rieman's genetical explanation. Three pairs of genes were involved in the development of pigment, namely:

1. C-c, a basic color factor, the dominant C gene being necessary for the production of any pigment, consequently, all cc plants produced white bulbs.
2. R-r, in the presence of C, the dominant R gene was responsible for the production of red pigment; its allele r was responsible for yellow pigment.
3. I-i, an inhibiting factor, I was partially dominant over i. All II plants produced white bulbs.

Red varieties carried the genes iCR, yellow varieties iCr, and recessive white might be either icR or icr. All varieties which carried the dominant inhibitor I were white, regardless of the presence or absence of the C and R factors.

Clarke, Jones and Little (36) said that their hypothesis fitted Rieman's data equally as well as did his multiple allele hypothesis and had the advantage of explaining certain results presented in their paper, which could not be accounted for by the assumption of multiple alleles. All the  $F_1$  plants from certain yellow  $\times$  recessive white crosses ( $ii\ GG\ rr \times ii\ oo\ RR$ ) had red bulbs. Furthermore, all three color classes segregated in the  $F_2$ , namely, red, yellow, and white (9:3:4). Since these results were contrary to those expected on Rieman's hypothesis, data on the color of bulb in the onion were interpreted on the basis of three independent pairs of factors:  $G-g$ ,  $R-r$ ,  $I-i$ .

Data of the present studies indicated the presence of a number of modifiers of the red-color intensity, each of which was producing an increasing effect when it existed in the dominant condition in red-color bulb varieties, presumably in the presence of the three major genes  $IGR$  suggested by Clarke, Jones and Little.

The environment was reported to exert an influence on bulb color. Knott (108, 109) studied the effect of some mineral elements on the color and thickness of onion scales. All varieties (of the yellowish-brown range) had thinner and poorer-colored scales on the areas which normally produced poorly-colored scales than on those which produced onions with good color (i.e. with a high degree of color for the variety). This indicated that the poor color of the scales was due to the environment and not to heredity. Data also indicated that either superphosphate or copper sulfate would improve



the thickness and color of onion scales. In another series of experiments, Knott (110) found that it was the copper and not the sulfate of the copper sulfate that was responsible for the thicker, better-colored scales.

In 1937, Binkley and Lorenz (18) found that onion bulbs of the Sweet Spanish variety produced on phosphate-treated plots were darker colored. Maturity, which was increased by phosphorus, probably had some effect on the color. Additions of manure and potassium produced the lightest colored bulbs.

Rain during the curing period tended to produce a dull dingy surface on all colors and, if excessive, tended to fade the outer scales of the yellows and reds (121).

Red varieties maturing under low temperatures were much more deeply colored than those maturing under high temperatures. The degree of bulb color of the strain Red 21 was found to vary somewhat with the locality, being much more intense in bulbs grown along the central coast (California) than in the interior valleys. The normal scale color was red and the flesh was pink (154).

Considering the influence of environment in general on bulb color in the present investigation, it was not so great as to interfere with the results obtained for genetical analysis. The best evidence for this was the fact that the material grown in Louisiana showed about the same segregation as the material grown in Colorado in a different growing season (Table XVI).

A knowledge of the relationship between the biochemistry of the plant pigments and the genetic factors for color inheritance is important. A brief review of some of the investigations on this subject is presented here. In general, the researches on the chemistry and genetics of color in plants indicate that in the inheritance of these pigments we are dealing with the inheritance of chemical compounds and chemical reactions.

The pigments of onion scales are solutes in the cell sap of the outer epidermal layer. Epidermal cells of yellow varieties turn a deep brownish-yellow when treated with alkalis, a reaction typical of flavones. Epidermal cells of red varieties turn pink in acid and green in alkaline solutions, which are characteristic reactions of anthocyanins (165).

Anthocyanins, or more generally anthocyanins, are coloring matters which are responsible for the red, violet, and blue pigmentations of flowers, of many fruits and to some extent of other plant tissues. It is known that crude extracts contain copigments such as tannin, gallic acid, etc. which possess the ability to intensify or modify the color (123).

Investigations on the biochemistry of flower-color variation in a number of species has shown that at least seventeen types of variation are involved (173). These types of variation are:

- I- Plastid pigment
  - a. Production
  - b. Inhibition

## II- Sap pigment production

- a. Anthoxanthin (flavone or flavonol) and anthocyanin
- b. Yellow anthoxanthin
- c. Ivory anthoxanthin, co-pigment
- d. General anthocyanin
- e. Specific anthocyanin

## III- Sap pigment regulation

- a. General intensification
- b. General suppression
- c. Local intensification (including normal allelomorphs of flaking, marbling, etc.)
- d. Local suppression

## IV- Anthocyanin modification

- a. Oxidation
- b. Oxidation and methylation
- c. Methylation
- d. Glycosidic change
- e. Acylation

## V- Localized acid pH.

"General" and "specific" types of anthocyanin production are quite distinct. They can occur both separately and together. "General" anthocyanin production is influenced in its nature and intensity by the modifying genes involving a more oxidized and/or more methylated pigment, the less oxidized types always being paler relative to the more oxidized. Mixtures of anthocyanin types never occur unless specific anthocyanin production is also involved. Both the nature and intensity of "specific" anthocyanin production is entirely independent of modifying genes for oxidation and methylation. With the exception of the effects of sharing a common precursor, it is also independent of any gene for general anthocyanin production which may be present.

A certain uniformity of behavior has been found amongst the genes analysed (173). For instance:

1. Plastid pigment, co-pigment, anthoxanthin, and both general and specific anthocyanin production are generally dominant to their absence, but rarely a dominant inhibiting factor is involved.

2. Modification involving more oxidized anthocyanin pigmentation is dominant to less oxidized.

Lawrence and Price (113) arbitrarily separated the action of genes involved in pigment production into "qualitative" and "quantitative". The former refers to the production or nonproduction of a pigment and the latter to difference in the amount of pigment. Inherited chemical differences originate in two ways: first from gene action, i.e. the action of a gene in relation to that of its allelomorph, and secondarily from gene interaction, i.e. the action of a gene in relation to that of nonhomologous genes. These relationships are interdependent, and together they are the determinants of dominance, and sometimes epistasy. Pigment production is genetically controlled, and in a number of cases complementary genes are involved. Variation in the amount of any pigment is also gene controlled. Such quantitative differences can be interpreted in terms of the velocity of the reactions involved in pigment production.

Modifications of the chemical structure of anthocyanins, including the state of oxidation, glycosidal type and probably the degree of methylation are each determined by simple gene relationships. In certain cases reactions are incomplete, giving rise to mixtures of anthocyanins (113).

Lawrence and Price (113), in their discussion of the genetics and chemistry of flower color variation, mentioned that large numbers of chemical reactions, some more or less independent, others parallel or sequential, are proceeding simultaneously in every cell of a living organism. If we consider the possibilities for any single reaction, then a gene can be controlling this reaction in one of the following ways:

1. In controlling supplies of the necessary reactants (such as a gene might control a previous stage in the synthesis, or the permeability of the cells).
2. In removing the reaction product—this would, for example, be necessary in a balanced reaction with an equilibrium point favoring the starting material.
3. In supplying an enzyme or other catalyst.
4. In controlling conditions, such as pH, which if unfavorable may lower the reaction velocity or even completely inhibit the reaction.

Lewis and Crane (115) described the mode of inheritance of a "purple anthocyanin" character in apples. Malus Neidzwetzkyana (purple) was found to differ from M. Malus (green) in having a single dominant gene for "purple pigmentation". Great variation was found within the "purple" plants, probably due to the segregation of modifiers.

Blank (21), in his review of anthocyanin pigments, stated that in the majority of cases observed the anthocyanins are present in solution in the cell sap. They have also been ascertained in the cell plasma of Allium Cepa. The various colors of tissues containing anthocyanins are not due alone to the various anthocyanins (e.g. cyanin, malin). The presence of anthocyanins in changing amounts and mixtures, alterations in the pH of the cell sap, the variable ash content of the latter, and above all co-pigmentation and the colloidal condition of certain components of the cell sap are all factors influencing the color of the anthocyanins dissolved in the sap. Investigations on the heredity of anthocyanins in flower petals are concerned with:

- a. genes controlling pigment production,
- b. genes controlling modification in anthocyanin type, and
- c. genes controlling the condition of the cell sap.

From the above discussion of the chemistry and inheritance of anthocyanins, which are present in red-color onion bulbs, it is safe to conclude that in case of onion-bulb color any variation in the intensity of the red color would be controlled by genes.

Two examples are given hereafter as evidence for the presence of modifiers of pigments other than anthocyanins.

Thompson (191) found that the dark-green chlorophyll color (GG) in lettuce leaves was found to act as a monogenic dominant to yellow-green (gg). He realized the possibility of existence of a third chlorophyll type intermediate between the dark green and yellow

green. Such a type is represented by some lettuce varieties. Thompson blamed the environmental conditions for producing variations sufficient to make it difficult to determine whether or not an intermediate existed between the dark and yellow green in the material studied.

Fleming and Myers (63) assumed the following three series of factors to account for the flesh color in tomato:

1. Two "basic color" factors. T and R, for the carotenoid pigments, lycopene, carotene, and xanthophylls. T produces orange, R yellow, and TR red. The double recessive, tr, is yellow.

2. A multiple series of modifiers ( $M_1, M_2$  etc.), probably enzymatic in nature, which may change a "basic" yellow to a "synthetic" orange, or a "basic" orange to a "synthetic" red. These factors also account for the variation in intensity of color noted in red and orange fruits. The exact number of modifiers has not been determined, but the results indicate that there are at least four.

3. Two inhibitors. The factor G inhibits the action of the modifiers in producing "synthetic" red. The factor K has a similar action on yellow fruited plants, preventing the production of "synthetic" orange.

## INHERITANCE OF SCAPE PRODUCTION (BOLTING)

### Experimental Methods

Three separate series of studies were undertaken. In the first series, the percentages of plants bolted (bolters) in 14  $F_2$  populations and in the Red Greole and Calred varieties grown from seed, were recorded. Seeds were planted in September 1949, and the final record for the percentages of bolters was taken in May 1950.

In the second series, the percentages of bolters were recorded for the same populations, but these plants were grown from relatively small bulbs produced at Greeley, Colorado. The bulbs were set in the field in November 1950, and the final records for the percentages of bolters were taken in May 1951.

The total numbers of plants examined in the first and second series were 5,374 and 1,540, respectively. Data of both of these studies were subjected to statistical analysis.

The material included in the third series of studies consisted of bulbs (8 months old) of 10  $F_2$  populations, stored in cold and in common storage. The temperature in cold storage was 35° F., but it was variably high in common storage, according to temperatures that prevail in Louisiana during the months of June to October. Percentages of bolters were recorded in May 1951. Total plants examined



were 258 and 259 from bulbs kept in cold and common storage, respectively. Analysis of variance for percentage of bolters was used for determining variations.

### Experimental Results

Data of the first series are presented in Table XIX. The Calred variety never bolted, while Red Creole showed 24.77% of bolters. The mean of both varieties was 12.38%. No significant difference (at .05 level) was found between the mean of parents and means of crosses 950 x 945 and 949 x 946. On the other hand the mean of each of the crosses 944 x 945 and 946 x 945 was found to be significantly lower than the mean of parents.

When the means of the four crosses were compared with each other, a significant difference was found only between the mean of cross 946 x 945 and the mean of any other cross.

These data indicate that Red Creole was heterozygous for bolting habit and gave some gametes for the non-bolting character. Lots 102 and 103, of the cross 946 x 945, were of this type. The general trend was toward the conclusion that the non-bolting character showed absence of dominance. If the Red Creole is heterozygous, as suggested, selection for non-bolting in this variety could be made.

Data of the second series are presented in Table XX. Calred bulbs were not included in the test because seeds sent to Greeley, Colorado, failed to germinate. However, bulbs of this variety did not bolt at Baton Rouge. It should be mentioned here that material included in this study had not bolted before, but the figures of percentages of bolters are not comparable with those obtained in the first series because plants that constituted the first series were grown from seeds whereas plants in the second series were grown from small bulbs.

The mean of the two parents was 25.10% of bolters. No significant difference was found between this mean and the mean of any of the four crosses. When the means of the four crosses were compared with each other, no significant difference was found.

These data indicate that the non-bolting character showed absence of dominance. The heterozygosity of the Red Creole parent was not clearly shown in this series of studies, possibly because of the smaller number of  $F_2$  plants in the cross 946 x 945 which were tested.

The mean of bolting percentages of both parents, as observed in material grown from seed and in material grown from small bulbs, was diagrammed and presented with similar data for  $F_2$  populations of four crosses in Figure 6.

The nature of distribution in each case indicates a higher percentage of bolters in material grown from bulbs than in material grown from seed. The histogram shows that absence of dominance was characteristic of the mode of inheritance of the non-bolting character.

For various reasons, very little genetic information was obtained concerning bolting. One reason was that the Red Creole parent appeared to be heterozygous. Also the environment obviously was a major factor influencing bolting. No conclusion could be drawn concerning the number of genes involved or heritability.

Data on the effect of type of storage on the percentage of bolters are presented in Table XXI. The analysis of variance for the percentages of bolters is given in Table XXII.

The information obtained from the analysis of variance shows that the differences between the two types of storage (treatments) are significant. There are also significant differences among the ten  $F_2$  populations. It is concluded that bulbs stored in cold storage showed a significantly lower percentage of bolters than those bulbs which were stored in common storage. In any given type of storage some of the  $F_2$  populations responded significantly different from others in regard to percentage of scapes produced.

Data, presented in Table XXIII, were obtained for demonstrating the effect of foliage reaction to mildew infection on the percentage of bolters. A total of 493 plants were tested in this study, bulbs of which were kept in cold storage.

These data indicate that in any given cross plants having susceptible foliage produced, in both years, approximately the same percentages of scapes as those plants which possessed moderately resistant foliage. Hence, the degree of foliage infection in the first growing season is thought to have no influence on the percentage of scapes produced in the second growing season from bulbs kept in cold storage.

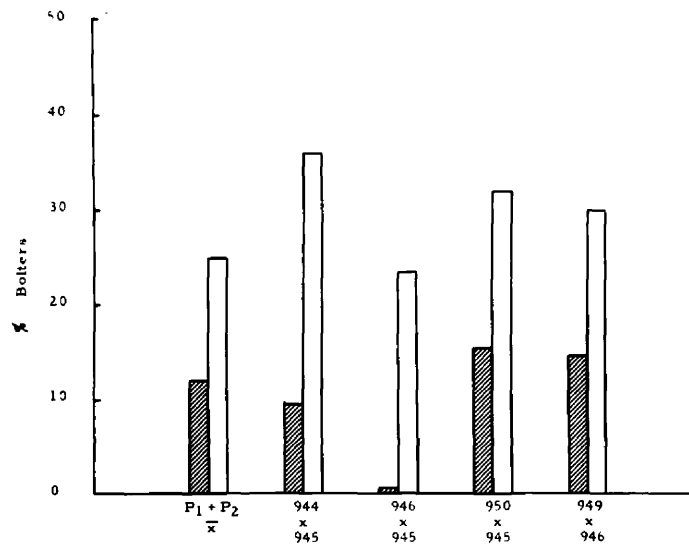


Fig. 6. Histogram showing the distribution of mean percentage of bolters in  $F_2$  populations and in parental varieties. (Striped bars = material grown from seed. White bars = material grown from small bulbs).





Table XXI. OCCURRENCE OF BOLTING IN TEN  $F_2$  POPULATIONS GROWN FROM BULBS

			% Bolters from bulbs stored in	
Lot	Pedigree		Cold storage	Common storage
Galred x Red Greele				
100	944	945	70.45	76.92
102	946	945	71.43	77.76
109	950	945	26.67	70.83
110	"	"	60.00	46.52
111	"	"	41.67	55.00
112	"	"	20.00	44.44
113	"	"	66.67	70.83
Red Greele x Galred				
104	949	946	76.47	76.00
106	"	"	92.86	100.00
107	"	"	50.00	80.00

Table XXII. SUMMARY OF THE ANALYSIS OF VARIANCE FOR PERCENTAGE OF BOLTERS

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Treatments	1	745.42	745.42	5.439*
$F_2$ populations	9	6067.50	674.17	4.919*
Error	9	1233.34	137.04	
Total	19	8046.26		

\* Significant at .05 level



Table XXIII. OCCURRENCE OF BOLTING IN FOUR F<sub>2</sub> POPULATIONS GROWN FOR TWO SUCCESSIVE SEASONS\*

Lot	Pedigree		Population	% Bolters in		Total of bolters in both years	
				1950	1951	No.	%
101	Calred x Red Greole 944      945		193 (a)	8.29	48.70	110	56.99
			26 (b)	11.54	30.77	11	42.31
			<u>219</u>	8.67	46.57	<u>121</u>	55.25
103	946      945		39 (a)	0.00	38.46	15	38.46
			8 (b)	0.00	37.50	3	37.50
			<u>47</u>	0.00	38.30	<u>18</u>	38.30
108	950      945		95 (a)	16.84	46.31	60	63.16
			3 (b)	0.00	66.67	2	66.67
			<u>98</u>	16.33	46.94	<u>62</u>	63.26
105	Red Greole x Calred 949      946		115 (a)	21.74	64.35	99	86.09
			14 (b)	7.14	78.57	12	85.71
			<u>129</u>	20.15	65.89	<u>111</u>	86.05

(a) Bulbs from plants having susceptible foliage

(b) Bulbs from plants having moderately resistant foliage

\* Seeds were planted in the first season, 1950.

Bulbs produced in 1950 and kept over summer in cold storage were used in the second growing season, 1951.

### Discussion and Literature Review

Under ordinary conditions, the onion bulb crop in the South is harvested in April or May. To obtain seed from the bulbs, the latter need to pass through a rest period in storage during the summer, after which they are planted in November. Seed from these bulbs is obtained in May or June of the following year. Under these conditions of culture, the onion plant completes its life cycle in about 22 months (80).

It is well recognized that varieties of onions differ in bolting habit (i.e. scape production). Low temperature during the development of the plant is known to be a most important factor in determining whether or not onions will bolt. However, recent data presented by Scully, Parker and Borthwick (175) indicate that photoperiod may also play a prominent role. Onion plants of sister lines differed in their production and development of visible scapes. Development of scapes was favored by long photoperiods.

Plant breeders and phytopathologists desirous of producing successive generations in the shortest time possible can grow their onions from seed to seed without an intervening dormant period if the environment is correctly manipulated. If this is to be done, the seedling should be started and maintained on a photoperiod below the critical one for bulbing. After the plants have grown for several months at relatively low temperatures, the photoperiod can be lengthened to promote flowering, but must not be lengthened so much that the plants will produce mature bulbs without flowering. High concentrations of

nitrogen added at this time help to depress the bolting tendency resulting from the longer photoperiod (175).

Probably one of the most striking examples of the interaction of genes with environment to produce a character is found in the bolting character of the onion.

Jones and Emsweller (96) were the first to report on the inheritance of bolting versus non-bolting in onion. In 1935, first-generation hybrids between the Italian Red male-sterile 13-53 and Lord Howe Island were grown in different localities in central California. None of the 13-53 plants bolted, and only 3.7% of the  $F_1$ , but 59.7% of the Lord Howe Island plants bolted. These data indicate that the non-bolting character in this cross is dominant. In another cross, viz. 13-53 x California Early Red U.C. 1, the non-bolting character also was dominant. In 1944, Jones and Davis (93) stated that the non-bolting character of Italian Red 13-53 behaved as an incomplete dominant. The hybrid Italian Red 13-53 x Lord Howe Island bolted a great deal less than Lord Howe Island, and the difference was highly significant.

Other conditions being equal, temperature plays an important part in the expression of the bolting habit. The percentage of bolters was very much higher in a location with a low average temperature than in a location with a high average temperature (96).

The present studies in which  $F_2$  populations were tested, indicate that percentage of bolters, on the average, in these populations did not show any significant deviation from the mean of both parents, being more or less intermediate between the two parental

varieties. This has been interpreted as a case in which dominance is absent, and it is concluded that the non-bolting character in the material studied showed absence of dominance. The Red Creele variety showed heterozygosity.

Montelaro (128a) found the Creele variety to be heterozygous in regard to the production of scapes. He mentioned that inbred lines of Creele selected for non-bolting had a smaller percentage of premature seeders (bolters).

The tendency of onion plants to bolt is shown from the literature to be influenced by the environment. In 1923, Boswell (24) found that bulbs stored at 50° F. produced the highest percentage of seeders and at 32° the percentage was markedly reduced. Jones (85), experimenting with the Ebenezer onion in 1927, found that bulbs stored at 7.5° C. and 11-12° C. produced a larger number of scapes than bulbs stored at either higher or lower temperature.

In 1939, Jones and Emsweller (97) stated that the best temperature for mother-bulb storage appeared to be about 45° to 55° F. Both high and low storage temperatures inhibited production of scapes and seed yield. Other factors known to influence the number of scapes formed and the yield of seed are size of mother bulb, spacing, and time of planting.

Recently, Woodbury (226) mentioned that the most effective storage temperature for inducing floral initiation was 50° F. The length of the storage period had no effect upon floral initiation in bulbs used in a greenhouse experiment.

The ability of the onion plant to flower under the Philippine conditions seemed to be a varietal characteristic. The flowering was

accelerated by storing the mother bulb first in cold storage ( $10^{\circ}$  C.) for a period of 25 to 71 days (167).

In central California, Jones, Poole and Emsweller (99) found that the percentage of bolting was high when a cool spring followed a warm fall. A warm fall caused a large plant to develop. This size and cool spring weather provided the proper combination of conditions for bolting. Because of the lower temperatures prevailing along the central California coast, bolting was more prevalent there than in the interior valleys, making it an ideal place to select and breed non-bolting strains that might be useful elsewhere.

Magruder et al. (121) mentioned that in the case of seedlings or green plants, the larger the plant at the time low temperatures occurred the higher the percentage of seeders. Varieties differed in their scape-producing ability under the same set of conditions.

The amount of bolting in the transplanted crop was determined by the interaction of a number of different factors (98). Certain varieties tended to bolt much more readily than others. Red Greole bolted rather readily. Calred did not bolt so readily. The size of the transplanted seedling also played a very important part, as large seedlings bolted much more readily than smaller ones (47). Temperature was particularly concerned in determining the amount of bolting. The highest percentage of bolting occurred after a warm late fall and a cold late spring. A warm fall favored the development of a large plant for overwintering, and the combination of a large plant and a cool spring provided ideal conditions for bolting. Conversely, the fewest bolters occurred after a cool fall and a warm spring. More bolt-

ing occurred on heavy than on light soils. In south Texas a few days delay in time of seeding in the nursery or in transplanting would often reduce considerably the amount of bolting (98).

In 1946, Heath and Holdsworth (74) stated that inflorescence initiation was apparently independent of day length and of bulb development but was very sensitive to temperature. Inflorescence emergence (i.e. bolting) was suppressed by bulb development, but was hastened by long days if the temperature conditions were such as to prevent the long days from causing rapid bulbing. These investigators postulated two hormone systems, viz.



E and F are both destroyed by high temperatures and both promote inflorescence initiation, but only E can cause the further initiation of flowers which stimulate auxin production and hence leads to emergence of the inflorescence. A is a bulbing hormone precursor and itself acts as an inhibitor for cell division in the blades of newly-initiated leaves. B, the active bulbing hormone, also acts as an auxin inhibitor. C is a leaf-growth hormone, but also stimulates auxin production.

Later, Holdsworth and Heath (77) summarized the effects of several factors tested on inflorescence initiation as follows:

1. There may be a minimum leaf number below which initiation cannot take place.
2. There is a minimum plant size below which initiation cannot take place.
3. There is a maximum temperature above which initiation cannot take place.

4. Day-length does not directly affect inflorescence initiation.
5. Bulb formation does not directly affect inflorescence initiation but may destroy inflorescences newly initiated.

## STORAGE QUALITY OF HYBRIDS

### A. Experimental Methods

The hybrid material was harvested when the tops fell down. Bulbs were cured on benches in the greenhouse for a few days, after which the tops were clipped. The bulbs were stored in two separate rooms especially built for storage investigations conducted by the Horticultural Research Department (L.S.U.). In the cold storage room temperature was around 35° F. The circulation of cold air was very much noticed. The temperature in the common storage room was about 90° F. during a large part of the storage period.

Data were recorded for material grown in the field during the seasons of 1949-50 and 1950-51. In cold storage the bulbs were stored individually, but they were in bulk in crates under common storage conditions. Generally, the bulbs were placed in storage during May and June. They were examined during the storage period a number of times. The rots and sprouted rots were discarded after being counted. Diseases observed in storage were described. Some effort was made to identify the causal organisms by examining the diseased tissues and by preparing spore mounts for microscopic examination. In some cases fungi which incited the rotting were cultured on potato dextrose agar or Czapek's agar medium.



Storage losses were estimated from the percentage of bulbs attacked by storage-rot organisms and rotted (referred to as rots), and the percentage of bulbs that were rotted and showed signs of sprouting (referred to as sprouted rots).

Toward the end of the storage period the percentages of sprouts among healthy bulbs--those which were obviously free from diseases--were recorded. Data on the percentages of sprouts were analysed statistically, but not extensively, because the nature of the material studied did not permit extensive analysis.

### B. Experimental Results

#### Length of Dormancy

##### 1950 Experiment:

The dormant and sprouted bulbs of fourteen  $F_2$  populations from different crosses, and the parental varieties were counted after 17 weeks in cold storage. A total of 1,322 bulbs was examined (Table XXIV).

Galred had 100 percent of bulbs sprouted, while the sprouted bulbs of Red Creole constituted only 34.4 percent.  $F_2$  populations varied in amount of sprouting between the two extremes, with the exception of lots 105 and 108, in which the percentages of sprouts were rather close, being 29.8 and 20.1 percent, respectively.

The mean value for parents was 67.2 percent of sprouts. This mean was found non-significantly different from the mean of any of the progeny of the four crosses. That is, bulbs of an  $F_2$  population had a dormancy period which was more or less intermediate in length between those of the two parents, indicating that the sprouting character showed absence of dominance.

##### 1951 Experiment:

Two separate studies were made. In the first study (Table XXV), a total of 893 bulbs of five  $F_2$  populations from one cross and the parental varieties were examined after 20 weeks in cold storage. After the same storage period, but in common storage, a total of 567 bulbs of seven  $F_2$  populations from the same cross (viz. 949 x 946)

and bulbs of the Red Creole parent were examined in the second study (Table XXVI).

The data indicated that Calred had 100 percent of sprouts and the Red Creole had only 18.6 percent in cold storage. The mean of parents was 59.3 percent, and the mean of the  $F_2$  populations was 29.9 percent.

The mean of the  $F_2$  populations was found to be significantly different (at .05 level) from the mean of the parents. Similar results were obtained from material kept in common storage in which the mean of parents was 66.5 percent and the mean of  $F_2$  populations was 28.6 percent. This would be an indication of heterozygosity in the Red Creole plant (viz. #949) used in the cross.

If the Red Creole variety is heterozygous for length of dormancy, as has been suggested, selection for late-sprouting Creole strains can be made.

Data on the percentage of sprouts in both types of storage are not comparable. One of the reasons for this non-comparability is the fact that, under cold storage or common storage conditions, the Calred parent reached the level of 100 percent of sprouts in storage after a shorter period than with the Red Creole. However, the heterozygosity of Red Creole parent was obvious, since there was a wide variation in the percentage of sprouts among the different  $F_2$  populations, descendant from the same cross, especially under common storage conditions.

Relatively little genetic information could be obtained regarding length of dormancy. No conclusion could be reached concerning the number of genes involved or heritability. The environment apparently had a major influence on length of dormancy.

### Storage Diseases

At least five different diseases were found in storage. These were black mold, blue mold, neck rot, *Fusarium* basal rot, and bacterial soft rots. For description of these diseases several references (viz. 157, 212, 215) were consulted.

#### Black Mold:

The chief sign of this disease was the presence of black, powdery spore masses of the fungus on the outside scale or between that and the next inner one. When these masses occurred between the scales, they tended to follow the veins (Plate XII). Under dry conditions the affected tissues were dry and papery (Plate XIII). This disease was found more prevalent in common storage than in cold storage.

The causal organism was *Aspergillus niger* v. Tiegh. Another *Aspergillus* species was isolated from the dry outer scales. It gave the infected scales a rather greenish appearance (Plate XIV). Apparently it grew as a saprophyte, and was extensively found under common storage conditions.

### Blue Mold:

The early symptoms were light yellow lesions which appeared on the outer fleshy scale. A whitish extramatrical mold followed which became blue green as the fungus sporulated (Plate XV).

This disease was known to be incited by a *Penicillium* species. An effort was made to isolate the causal organism in a pure culture from rotted bulbs kept in cold storage. The species was kindly identified by Dr. K. B. Raper (1959) as *P. cyclopium* Westling. Healthy bulbs, artificially inoculated by this species, showed the typical blue mold symptoms (Plate XVI).

### Neck Rot:

The first sign of gray-mold neck rot was the softening of the affected scale tissue, which took on a sunken, cooked appearance. As the mycelium increased in the older diseased area, the tissue became grayish in color, and later a dense, grayish mycelial mat often developed upon the surface of the scales. Under moderately humid conditions conidial production was prompt. A dense layer of gray mold appeared which consisted of conidiophores and myriads of conidia (Plate XVII). In connection with the older decayed tissue, sclerotia appeared (Plate XVIII). While the host tissue in the beginning of its decay was somewhat watery, it desiccated rather promptly. The moisture which was released was often sufficient to stimulate premature sprouting. The older decayed bulb presented the appearance of a "mummy".

Almost an epiphytotic of the gray-mold neck rot disease, incited by Botrytis allii Munn., was developed in cold storage in 1951 (Table XXX). Dissemination of spores was effected by the powerfully circulated air in the cold storage room. A percentage of infection as high as 64.2% was recorded.

Neck rot disease or diseases are incited by three different fungi. Botrytis allii Munn. incites the gray-mold neck rot. B. hyssoides J. C. Walker incites the mycelial neck rot. B. squamosa J. C. Walker incites the small-sclerotial neck rot. The gray-mold neck rot disease was the only one found during the present studies.

#### Fusarium Basal Rot:

At the base of the bulb a whitish or pinkish moldy growth appeared on the surface of decayed portions of the scale. In severe cases the bulb might show a semiwatery, a mealy, or a dry decay which progressed along the scales from the base upward (Plate XIX).

The causal organism was Fusarium oxysporium Schlecht.

#### Bacterial Soft Rots:

The affected tissues were glassy or water-soaked at first, later becoming soft and mushy. The decay was often confined to one or two scales in the interior or to the central scales. The diseased bulbs could be detected by gently pressing them, whereupon the watery fluid was extruded through the neck. The slimy decay was usually accompanied by a foul sulfurous odor.

Sour skin was a decay that affected only certain of the outer fleshy scales. The rot was slimy and yellow and gave off a vinegar-like odor. The scales outside the rotting ones slipped off readily in handling.

The causal organisms were not identified. Walker (215) stated: "The bacterial-soft-rot organism, Erwinia carotovora (L. R. Jones) Holland, is the incitant usually cited, but is relatively uncommon as an onion pathogen in nature.

Pseudomonas alliiicola Berk. and P. cepacia Burk. were also found as pathogens inciting bacterial soft-rot and sour skin in onion, respectively."

#### Storage Losses

##### 1950 Experiment:

Totals of 2,445 and 1,689 bulbs were stored in common storage and cold storage, respectively. The percentages of rots and of sprouted rots were recorded after 3, 8, 12 and 17 weeks in storage. The material tested was grown from seeds planted in the fall of 1949, and consisted of 14  $F_2$  populations and the parent varieties, Red Creole and Calred.

Data, presented in Table XXVII, indicated that minimum and maximum losses after 17 weeks in cold storage were 1.4% and 50.0%, while in common storage they were 66.2% and 95.2%, respectively. The percentages of rots and sprouted rots increased as the length of the storage period increased. This was not true for bulbs kept in cold storage, where no

rot was observed after 8 weeks, except lot 108, in which a very slight increase in the amount of rot was recorded.

In common storage, the Red Creole variety showed the least loss (i.e. 66.2%), while the Calred showed the highest loss (i.e. 95.2%).

The effect of mildew on the keeping quality of onion bulbs may be demonstrated by comparing bulbs of some  $F_2$  populations such as lot 101 or lot 105, stored in cold storage. In each lot the percentage of storage loss among bulbs produced by plants having moderately resistant foliage was relatively lower than among bulbs produced by plants having susceptible foliage. In other lots (e.g. lot 105) the difference was apparently nonsignificant.

#### 1951 Experiments:

Two separate studies were made. In the first study, totals of 2,099 and 1,367 bulbs were stored in cold storage and common storage, respectively. The percentages of rots and of sprouted rots were recorded after 3, 10 and 20 weeks in storage (Tables XXVIII, XXIX). The material tested was grown from seeds planted in the fall of 1950, and consisted of 15  $F_2$  populations from the cross 949 x 946 and the parental varieties. It should be mentioned that the  $F_2$  populations stored in cold storage (8 in number) were other than those stored in common storage (7 in number). The Calred parent was not placed in common storage because an almost total loss was encountered when Calred bulbs were stored under such conditions.

The data indicated that the Red Creole variety showed 29.6 percent of rots and sprouted rots after 20 weeks in cold storage, whereas the Calred exhibited 76.7%. This percentage varied from 21.5 to



71.7 in the second generation populations. In common storage, after the same storage period, Red Creole showed only 17.3%, and  $F_2$  populations exhibited a range of 41.6% to 78.2%. The percentages of rots and of sprouted rots found in cold storage was much higher than was expected. For instance, the Red Creole variety (which proved to be a good-keeper) showed in cold storage a higher percentage of losses (viz. 29.6%) than in common storage where the amount of loss was 17.3%. It was also surprising to find that the increase in percentage of storage losses during the period extended from the 10th week to the 20th week was very much higher in cold storage than in common storage. The cause of such misleading discrepancies was the spread of *Botrytis* infection in cold storage during the last part of the storage period.

Table XXX shows the percentage of rots, in cold storage, due to infection by *Botrytis allii* and other storage-rot organisms. Populations selected for this study were five  $F_2$ , two first backcrosses, and the two parental varieties. A total of 1,513 bulbs was examined. The results indicated that the Calred variety (which proved to be a poor keeper) did not show any infection by *Botrytis*. However, this variety sprouted badly and infection was recorded as sprouted rots. The average percentage of *Botrytis* rots was 29.8% among  $F_2$  populations, whereas the percentages of rots due to other organisms was as low as 0.6%. This would clearly indicate the aggressiveness of *Botrytis allii* in cold storage where conditions were in favor of its development, especially the high relative humidity which was frequently recorded.

Data on the first backcross populations were interesting. During the critical period that extended from the 10th week to the 20th week in cold storage, losses caused by *Botrytis* infection were

sharply increasing among  $F_2$  populations. The average percentage of total rots among these populations was 30.4, and the Red Creole showed 19.6%. On the other hand, the two first backcross populations were showing a distinctly low percentage of losses, viz. 4.3 and 9.9 percent of rots due to various storage-rot organisms. These results indicated that through backcrossing, using the Red Creole as the recurrent parent, some improvement of the storage quality was achieved by reducing the percentage of rots.

Data of the second, separate study are presented in Tables XXXI and XXXII. This study was made in an effort to answer the question as to whether or not bulbs from bolted plants would have the same storage quality as bulbs from non-bolted plants. Taking into consideration the number of bulbs tested, lots 100, 104, and 105 (Table XXXI) were closely examined. There was not any appreciable difference between the percentages of rots among bolted and non-bolted bulbs, after 16 weeks in cold storage. It was thought that bulbs of bolted plants might keep as well as bulbs of non-bolted plants.

Table XXIV. PERCENTAGE OF SPROUTS AMONG HEALTHY BULBS OF CALRED, RED CREOLE, AND 14 F<sub>2</sub> POPULATIONS, STORED IN COLD STORAGE FOR 17 WEEKS. 1950

Lot	Pedigree		Bulbs examined No.	Number of Bulbs Dormant Sprouted		% Sprouts	$\bar{x}$	s	$\bar{sx}$
	Calred x Red Creole								
100	944	945	161	86	75	46.6			
101	"	"	363	152	211	<u>58.1</u>	52.3	8.13	5.75
102	946	945	27	12	15	55.5			
103	"	"	127	82	45	<u>35.4</u>	45.4	14.21	10.05
108	950	945	194	155	39	20.1			
109	"	"	36	16	20	55.5			
110	"	"	24	7	17	70.8			
111	"	"	30	13	17	56.7			
112	"	"	7	3	4	57.1			
113	"	"	12	5	7	<u>58.3</u>	53.1	17.11	6.99
	Red Creole x Calred								
104	949	946	26	12	14	53.8			
105	"	"	211	148	63	29.8			
106	"	"	25	13	12	48.0			
107	"	"	14	4	10	<u>71.4</u>	50.7	17.15	8.57
114	Calred		33	0	33	100.0			
115	Red Creole		32	21	11	<u>34.4</u>	67.2		

Table XXV. PERCENTAGE OF SPROUTS AMONG HEALTHY BULBS OF CALRED, RED CREOLE, AND 5 F<sub>2</sub> POPULATIONS, STORED IN COLD STORAGE FOR 20 WEEKS. 1951

Lot	Pedigree		Bulbs examined	Number of Bulbs		% Sprouts	$\bar{x}$	s	$\bar{sx}$
			No.	Dormant	Sprouted				
	Red Creole x Calred								
1	949	946	63	55	8	12.7			
2	"	"	194	138	56	28.9			
3	"	"	246	174	72	29.3			
8	"	"	135	71	64	47.4			
11	"	"	45	31	14	<u>31.1</u>			
							29.9	12.3	5.50
30	Calred		22	0	22	100.0			
32	Red Creole		188	153	35	<u>18.6</u>			
							59.3		

Table XXVI. PERCENTAGE OF SPROUTS AMONG HEALTHY BULBS OF RED CREOLE, AND 7 F<sub>2</sub> POPULATIONS, STORED IN COMMON STORAGE FOR 20 WEEKS. 1951

Lot	Pedigree	Bulbs examined No.	Number of Bulbs		% Sprouts	$\bar{x}$	s	$s\bar{x}$
			Dormant	Sprouted				
	Red Creole x Calred							
4	949      946	9	9	0	0.0			
5	"      "	41	30	11	26.8			
6	"      "	74	44	30	40.5			
9	"      "	146	80	66	45.2			
10	"      "	89	66	23	25.8			
12	"      "	20	18	2	10.0			
14	"      "	73	35	38	52.0			
						28.6	18.88	7.13
32	Red Creole	115	77	38	33.0			
—	Calred, assumed to show				100.0			
						66.5		

Table XXVII. STORAGE DATA - PARENTS AND F<sub>2</sub> POPULATIONS GROWN IN 1949-50 SEASON, HARVESTED, CURED, AND STORED IN COMMON STORAGE AND COLD STORAGE FOR DIFFERENT PERIODS

Lot	Pedigree	COMMON STORAGE					COLD STORAGE					
		Bulbs stored No.	Accumulative % rots and sprouted rots after				Bulbs stored No.	Accumulative % rots and sprouted rots after				
			Weeks					Weeks				
			3	8	12	17		3	8	12	17	
Calred x Red Greole												
100	944	945	538	64.7	75.1	82.1	82.9	220 (R)	25.9	26.8	26.8	26.8
101	"	"	-	-	-	-	-	43 (R)	0.0	2.3	2.3	2.3
			-	-	-	-	-	473	38.3	38.7	38.7	38.7
102	946	945	74	55.4	71.6	79.7	83.8	33 (R)	15.1	18.2	18.2	18.2
103	"	"	-	-	-	-	-	19 (R)	0.0	5.3	5.3	5.3
			-	-	-	-	-	139	56.8	58.3	58.3	58.3
108	950	945	-	-	-	-	-	8 (R)	37.5	50.0	50.0	50.0
			-	-	-	-	-	252	36.9	37.7	37.7	38.1
109	"	"	449	55.4	74.8	78.8	80.4	45 (R)	20.0	20.0	20.0	20.0
110	"	"	246	54.5	66.3	74.8	77.6	31 (R)	22.6	22.6	22.6	22.6
111	"	"	233	36.5	68.2	76.0	78.1	50 (R)	38.0	40.0	40.0	40.0
112	"	"	85	64.7	84.7	91.8	91.8	12 (R)	4.2	4.2	4.2	4.2
113	"	"	281	60.1	84.3	87.9	88.6	14 (R)	1.4	1.4	1.4	1.4
Red Greole x Calred												
104	949	946	229	40.2	68.1	76.8	79.9	28 (R)	7.1	7.1	7.1	7.1
105	"	"	-	-	-	-	-	22 (R)	27.3	27.3	27.3	27.3
			-	-	-	-	-	194	30.9	30.9	30.9	30.9
106	"	"	157	63.7	86.6	92.3	94.3	33 (R)	21.2	24.2	24.2	24.2
107	"	"	58	48.3	79.3	82.7	86.2	15 (R)	0.0	6.7	6.7	6.7
114	Calred		21	66.7	90.5	95.2	95.2	29	27.6	27.6	27.6	27.6*
115	Red Greole		74	31.1	54.0	64.9	66.2	29	48.3	48.3	48.3	48.3

- indicates data not available.

\* Bulbs in cold storage were sprouting but not rotting.

(R) Resistant plants; foliage moderately resistant.

Table XXVIII. STORAGE DATA - PARENTS AND  $F_2$  POPULATIONS GROWN IN 1950-51 SEASON, HARVESTED, CURED, AND STORED IN GOLD STORAGE FOR DIFFERENT PERIODS

Lot	Pedigree	Bulbs stored No.	Accumulative % rots and sprouted rots after		
			Weeks		
			3	10	20
	Red Creole x Calred				
1	949 946	219	8.7	16.9	71.7
2	" "	326	10.4	13.8	41.7
3	" "	312	6.4	7.4	21.5
7	" "	292	4.8		
8	" "	180	0.5	3.9	26.1
11	" "	97	6.2	16.5	53.6
13	" "	180	11.7		
15	" "	160	6.2		
30	Calred	73	21.9	34.2	76.7
32	Red Creole	260	0.8	4.6	29.6

Table XXIX. STORAGE DATA - PARENTS AND  $F_2$  POPULATIONS GROWN IN 1950-51 SEASON, HARVESTED, CURED AND STORED IN COMMON STORAGE FOR DIFFERENT PERIODS

Lot	Pedigree	Bulbs stored No.	Accumulative % rots and sprouted rots after		
			Weeks		
			3	10	20
	Red Creole x Calred				
4	949 946	40	42.5	77.5	77.5
5	" "	188	44.7	76.6	78.2
6	" "	183	9.8	51.9	59.6
9	" "	250	21.2	40.4	41.6
10	" "	252	30.1	59.5	64.7
12	" "	72	36.1	68.0	72.2
14	" "	243	38.3	65.4	69.9
32	Red Creole	139	3.6	14.4	17.3

Table XXX. STORAGE DATA - INCIDENCE OF BOTRYTIS ROTS IN BULBS\* OF THE PARENTS, F<sub>2</sub>, AND FIRST BACKCROSS POPULATIONS STORED IN COLD STORAGE, 1951

Lot	Pedigree	Bulbs examined No.	% rots due to infection by		
			Botrytis	Other organisms	Total
	Red Creole x Calred				
1	949      946	176	64.2	0.6	64.8
2	"      "	273	28.9	1.5	30.4
3	"      "	286	13.6	0.7	14.3
8	"      "	161	17.4	0.0	17.4
11	"      "	60	25.0	0.0	25.0
	Average		29.8	0.6	30.4
16	F <sub>1</sub> x Red Creole	139	2.1	2.1	4.3
17	F <sub>1</sub> x Red Creole	162	9.2	0.6	9.9
30	Calred	22	0.0	0.0	0.0
32	Red Creole	234	19.2	0.4	19.6
	Average		9.6	0.2	9.8

\*These bulbs were healthy after 10 weeks in storage, but were subjected to infection by air-blown spores during the subsequent 10 weeks. Percentage of sprouted rots are not included.



Table XXXI. STORAGE DATA - BULBS\* SET OUT IN FALL 1950, HARVESTED IN SPRING 1951, CURED, AND STORED IN COLD STORAGE FOR DIFFERENT PERIODS

Lot	Pedigree		Number of bulbs stored		Accumulative % rats after					
			Bolt.	Non Bolt.	3 weeks		10 weeks		16 weeks	
					Bolt.	Non Bolt.	Bolt.	Non Bolt.	Bolt.	Non Bolt.
Calred x Red Creole. F <sub>2</sub>										
100	944	945	45	35	0.0	2.8	8.9	8.6	8.9	11.4
101	"	"	7	91	14.3	4.4	14.3	16.5	14.3	16.5
102	946	945	11	8	9.1	0.0	9.1	12.5	9.1	12.5
103	"	"	7	44	28.6	27.3	28.6	38.6	57.1	40.9
108	950	945	-	38	-	5.3	-	7.9	-	7.9
109	"	"	-	22	-	31.8	-	40.9	-	40.9
110	"	"	-	26	-	3.8	-	19.2	-	19.2
111	"	"	-	13	-	0.0	-	23.1	-	30.8
113	"	"	-	6	-	0.0	-	0.0	-	0.0
Red Creole x Calred. F <sub>2</sub>										
104	949	946	13	15	7.7	0.0	7.7	6.7	7.7	6.7
105	"	"	24	24	0.0	0.0	0.0	0.0	0.0	0.0
106	"	"	5	-	0.0	-	0.0	-	0.0	-
114	Calred		-	8	-	0.0	-	0.0	-	0.0
115	Red Creole		-	15	-	6.7	-	6.7	-	6.7

- indicates data not available.

\*These bulbs were produced from seeds planted in fall of 1949 at Baton Rouge, La.

Table XXXII. STORAGE DATA - BULBS\* SET OUT IN FALL 1950, HARVESTED IN SPRING 1951, CURED, AND STORED IN COLD STORAGE FOR DIFFERENT PERIODS

Lot	Pedigree	Number of		Accumulative % rats after							
		bulbs stored		3 weeks		10 weeks		16 weeks			
		Bolt.	Non Bolt.	Bolt.	Non Bolt.	Bolt.	Non Bolt.	Bolt.	Non Bolt.		
Calred x Red Creole. F <sub>2</sub>											
100-C	944	945	13	96	0.0	2.1	7.7	8.3	23.1	15.6	
101-C	"	"	5	45	20.0	4.4	40.0	13.3	60.0	28.9	
102-C	946	945	5	34	0.0	5.9	20.0	5.9	20.0	14.7	
103-C	"	"	-	10	-	0.0	-	0.0	-	0.0	
108-C	950	945	10	105	0.0	1.9	10.0	9.5	20.0	28.6	
109-C	"	"	-	107	-	0.0	-	6.5	-	22.4	
110-C	"	"	-	33	-	6.1	-	9.1	-	48.5	
111-C	"	"	12	25	0.0	0.0	0.0	4.0	0.0	16.0	
112-C	"	"	-	16	-	6.2	-	12.5	-	18.7	
113-C	"	"	-	27	-	7.4	-	14.8	-	29.6	
Red Creole x Calred. F <sub>2</sub>											
104-C	949	946	-	15	-	6.7	-	20.0	-	26.7	
105-C	"	"	-	40	-	0.0	-	2.5	-	15.0	
106-C	"	"	14	54	0.0	1.8	7.1	3.7	21.4	14.8	
107-C	"	"	5	24	0.0	4.2	0.0	16.7	0.0	25.0	
115-C	Red Creole		-	108	-	7.4	-	18.5	-	28.7	

- indicates data not available.

\* These bulbs were produced from seeds planted in early spring 1950 at Greeley, Colo., and were stored during summer 1950 in cold storage.

## C. Discussion and Literature Review

### Length of Dormancy

One of the earliest investigations conducted by Dr. Jones was on onion dormancy (83). He found a great variation in the dormant period of individual bulbs within the Yellow Globe Danvers variety. While most of the bulbs started growth in 55 to 70 days, a few preceded the general average time, while a few remained dormant for 85 to 90 days. Observations made in the field on the relative dormant periods of different varieties, revealed the fact that some varieties have a dormant period considerably shorter than that of the Yellow Globe Danvers when handled similarly and these are notably those varieties that are notoriously poor storage onions.

In 1920, Dr. Jones wondered about the development of a strain of onions with a dormant period longer than the average for that variety. He said that this was possible if this character in all its intensity was transmitted to the progeny.

In 1952, the present investigations gave evidences that there were genetic factors determining the length of the dormancy period in onion, the exact number of which are not readily determined. However, data suggested the presence of but a few genes and perhaps just one pair of genes as differentiating the homozygous Calred and the heterozygous Red Creole parents. It was found that the length of dormancy period showed absence of dominance.

### Storage Diseases

Hatfield, Walker and Owen (71) mentioned that black mold was in one season significantly more severe on colored than on white varieties. Australian Brown, the most deeply colored variety, had the highest percentage of infected bulbs in two out of the three seasons in which the disease was quite extensive. The extract of dry outer colored scales was distinctly stimulative to germination and growth of Aspergillus niger, when compared with white outer scale extract. It appears that the same phenolic substances which were the major factors for resistance to smudge and which played a part in neck rot resistance might be the ones which contributed to black mold susceptibility in colored varieties. The extreme sensitivity of this organism to the volatile and nonvolatile antibiotics in the succulent scales of both white and colored varieties appeared to be a deterrent factor in restricting the organism to a superficial and extremely mild pathogenesis.

In 1917, Munn (134) reported on relative resistance of different varieties of onions to neck rot disease. It is a fact well known to onion growers that the thin-skinned white varieties suffer very severely from the neck rot (Botrytis allii). There appears to be but little difference between the relative resistance of the Red and Yellow Globe varieties. No difference in susceptibility to neck rot could be detected between the various shapes of onion bulbs; however, it was found that the extreme globe or "bottle neck" types were slower in drying out at the neck and consequently showed a greater percentage of neck rot.

Data presented by Nicolais and Scupin (142) showed that the natural drying of the onions in the field promoted resistance to storage infection (by B. allii) by firmly sealing the junction between the neck and bulb through which the fungi gained entrance. Onions attacked by downy mildew in the field were particularly liable to storage infection by B. allii.

In Netherlands, Beekun's results (13) supported the general view that the lighter colored varieties were much more susceptible to *Botrytis* neck rot than the darker, as indicated by the fact that the straw-yellow variety Bola developed 5.5 - 3.5 percent rot as against an average of 1.95 - 1.3 percent rot in four brown varieties.

In his early study on *Botrytis* neck rots in 1926, Walker (211) described three closely-related but distinct neck rot diseases of onion bulbs. They were distinguished as follows: gray-mold neck rot (*Botrytis allii*), mycelial neck rot (*B. byssoides*), and small sclerotial rot (*B. squamosa*). Up to that time, *B. squamosa* had been found in nature only on white bulbs, or (in one instance) on bulbs having a very slight yellowish color. The high resistance of yellow and red bulbs was shown by the fact that in several cases in which the small sclerotial neck rot occurred on white onions, colored bulbs grown next to them were completely free from the disease. There was abundant evidence, however, that colored bulbs were not resistant once infection was established. In nature they were not always completely free from the gray-mold or mycelial neck rots.

In 1948, Hatfield, Walker and Owen (71) mentioned that in the one year in which neck rot (B. allii) developed severely enough to permit the evaluation of the resistance of varieties there was no correlation between resistance and color, but a distinct correlation between strong pungency and resistance. Mild varieties of onion showed a higher percentage of infection than did strongly pungent varieties. Both of the volatile and nonvolatile antibiotics in fleshy scales of the mild varieties were less toxic to B. allii than those of the strong varieties. Thus the fleshy scale antibiotics probably were a factor in reducing the amount of neck rot infection in strongly pungent as compared with mild varieties.

The neck rot organism (B. allii), being primarily a wound invader, gained access usually at the neck of the bulb. It was sensitive to the phenol antibiotics in the outer scales, which had a partially restraining effect, although they were inclined to be less uniformly prevalent in the neck tissues than in the bulb proper. In many instances they did provide the resistant barrier commonly associated with colored varieties in relation to this disease. If the fungus became established in succulent tissue, however, resistance in relation to color no longer held (71).

An example of a severe infection by B. allii in colored hybrids was well illustrated in the present investigations.

In 1926, Link and Bailey (116) described several species of *Fusarium* found to cause onion bulb rot. Red, yellow, and white varieties were equally susceptible.

Self-pollinated selections (Red and Yellow Globe) showed differences in the degree of resistance, and four years of selfing and selecting yielded several strains that showed no bulb rot (Fusarium zonatum forma 1) in storage. Selection and inbreeding of Red and Yellow Globe onions resulted in the isolation of 5 strains in which the loss from bulb rot in the field and in storage was less than 5 percent in 1935 and 1936, when the loss in the checks was 90 percent (46).

The smudge disease, a well known storage trouble, incited by Colletotrichum circinans (Berk.) Vogl., was not found in the present storage studies, due perhaps to the fact that white bulbs were not included in the material tested. Hatfield, Walker and Owen (71) stated that the smudge organism was restricted to white varieties by its extreme sensitivity to the phenol antibiotics in dry outer scales of colored varieties except in those cases in which the outer scales slough or split so as to expose the fleshy scales. After infection of the succulent scales of colored or uncolored varieties, its progress is impeded by the volatile and nonvolatile antibiotics in the succulent tissue which appear to restrict its pathogenic action, but there is evidence that the fungus neutralizes these antibiotics to some extent. Jones et al. (101) showed that white bulbs homozygous for the dominant color inhibitor I were highly susceptible to smudge. Colored bulbs with the genetic constitution ii are highly resistant. Cream bulbs with the constitution Ii were approximately intermediate in resistance between the pure white and the colored ones.

Over a period of almost thirty years, Walker and his associates in Wisconsin have been investigating the interaction of color, pungency, and some other factors on the incidence of some onion di-

seases, namely, neck rot (B. allii), smudge (O. circinans), and black mold (A. niger). It was found, as reported in a recent contribution (145), that neck rot was more severe on mild than on pungent varieties. In the mild class there was no difference between colored and white varieties, while in the strong pungent class the colored varieties had significantly lower indices than white varieties.

Pungent varieties in each color group had lower smudge indices than mild varieties. White varieties had significantly higher indices than colored varieties.

In the case of smudge, in contrast to neck rot, the phenolic antibiotics associated with color (i.e. protocatechuic acid and Catechol) were much more influential than the antibiotics associated with pungency.

Pungency was not important in determining the incidence of black mold. Under dry conditions the disease was more severe than under moist conditions, but there was little difference in its development on white and on colored varieties. Under moist conditions colored varieties showed more black mold development than did white varieties (145).

Results obtained by Frierson (67) indicated that *Fusarium*, *Pythium*, *Phoma*, and *Rhizoctonia* were the fungi isolated most frequently from diseased onion roots in Louisiana. Species of *Sclerotium*, *Botrytis*, *Aspergillus*, *Pythium*, *Rhizoctonia*, and *Fusarium* were found commonly associated with diseased bulbs. *Fusarium* was most frequently isolated.



## Storage Quality of Onion Bulbs

Storage quality of the onion is a broad term, and may be applied to the behavior of bulbs or sets in storage. Many factors are known to affect the storage quality, some of which are

1. The influence of degree of maturity
2. The influence of storage conditions
3. The influence of moisture content
4. The influence of diseases

### Influence of degree of maturity:

Magruder et al. (120) mentioned that experience had shown that only normally matured, well-cured onions should be stored for any appreciable length of time. Normal maturity meant that maturity took place under favorable conditions for the general decline of root and leaf activity with a gradual softening of the neck and a transference of the soluble solids of the leaves into the bulb, so that the outer succulent layers of the bulbs nearly closed the opening over the leafless inner scales. Any cause of premature death of the leaves caused the neck of the bulbs to remain open and permitted the entrance of moisture and various rot organisms.

In 1923, Boswell (23,24) stated that late maturing onions sprouted in storage more readily than early maturing onions. Losses from decay were less in early maturing onions of the same variety. "Early" referred to those bulbs whose tops were first to fall over, while "late" referred to those bulbs whose tops did not go down until 3 or 4 weeks later.

Onions have a rest period of approximately two months, during which time growth is not likely to start, even though the temperature and moisture conditions are optimum for growth. Open and thick-neck bulbs soon resume growth (sprout) or rot. When decay is not a factor, quicker sprouting is thought to result from the greater accessibility to oxygen of the central growing point in the open or thick-neck bulbs than in the bulbs with well-closed necks (23,24).

Wilson's results (225) showed variation in keeping quality of the same variety during a 3-year period. Representative samples of many varieties were placed in common storage. A record was kept of the number of bulbs stored and the number marketable at time of examination. He concluded that keeping quality was influenced very greatly by degree of maturity and by curing. An immature bulb would not keep well in storage, neither would a bulb which had made a second growth, even though this growth was most apparent to external observation.

Results presented by Hoyle (78) stressed three factors which affected storage quality: first, the time of maturity at harvest; second, length of topping; and third, interaction between time of maturity and length of topping.

In 1927, Gaylord (70) recommended rigid grading at storage time and the placing of only bright, sound, high quality onions in storage. This would greatly reduce shrinkage loss. In 1925-26 the loss on sound, rigidly graded onions was 4.3%, while damp, green and poorly graded stock had a total percentage loss of 22.4.

Krickl (111) conducted experiments on breeding for late sprouting, and thus high keeping quality. As a rule there was a correlation between late sprouting, relatively little weight loss in storage, and high osmotic value. Onion bulbs with single centers should be selected, and the proportion of heart to outer scales should be considered.

In England, Croxall (42) reported that early lifting, in six varieties, before the tops had died down resulted in significantly less loss of bulbs in storage.

In India, Karmarkar and Joshi (104) stated that the state of maturity of the stored bulbs greatly influenced the loss in weight in storage at 90-95° F. Onions which were fully developed or completely 'capped over' at the time of harvesting lost the least in weight. The higher loss in weight from 'just mature' bulbs might be due to the thicker neck of the bulbs, permitting increased evaporation of moisture from the interior.

#### Influence of storage conditions:

Extensive studies were made by Magruder et al. (120). Because storage quality is one of the important commercial characteristics of the onion it was included in the list of characters studied in the United States Department of Agriculture Type Book project covering the principal American varieties of onions and conducted cooperatively during 1933 and 1934 by the U.S.D.A. and the State Experiment Stations of California, Ohio, and Texas, and the Massa-

Massachusetts State College. Crops were stored under different conditions for different lengths of time, but the same seeds were used by all collaborators.

As a result of the tests conducted during a 2-year period, some of the varieties tested may be placed in the following groups with reference to their suitability for storage:

Variety	Suitability for storage
Italian Red	Very poor
Crystal Wax	Poor
Yellow Bermuda	"
White Sweet Spanish	Fair
Ebeneser	Good
White Creole	Very good
Red Creole	" "
Australian Brown	" "

The majority of the losses were from neck rot, although there was a small percentage of side and basal rot. The Creole strains and Australian Brown were remarkably free from rots, sprouts, or shriveled and soft bulbs. Unlike the material in cold storage, the rots in the onions in room-temperature storage (65° - 75° F.) developed mostly at the base.

California results indicated that in most varieties rotting occurred during the early part of the storage period, but in California Early Red, Crystal Wax, and Early Grano, rotting was most prevalent during the latter part of the storage period. Rotting was most severe in Italian Red, Yellow Bermuda and other varieties that had a mild flavor and a low percentage of dry matter. The least rot occurred in the Red Creole, White Creole, and Australian Brown, all

highly pungent varieties. These observations suggested that components giving a high pungency might also have something to do with resistance to certain rot organisms.

Texas data indicated that Bermuda onions which were allowed to mature fully so that the tops became partially dry in the field before pulling did not keep as well as those that were harvested and clipped in the usual manner when only about 60 percent of the plant tops had fallen over. The poor keeping after later harvesting may be due to the fact that soil-inhabiting rot-producing organisms gained entrance through the dying roots or that the additional time in the soil might prevent the bulbs from becoming completely dormant.

Bulbs stored at high temperatures lost marketability faster than bulbs stored at low temperatures, as shown by the 1933 results at Amherst, Mass., and the 1934 results at Arlington, Va. At Arlington, where the high temperature ( $65^{\circ}$  -  $75^{\circ}$  F.) was rather uniform and higher than at Amherst, 2 months in storage at the high temperature caused about the same amount of loss as 9 months' storage at  $40^{\circ}$  F. During the same time interval at Amherst all of the varieties lost a greater percentage in the shed storage where the temperatures were higher and fluctuated more than they did in the cold storage where the relatively uniform temperature was about  $40^{\circ}$  F. (120).

Wright et al. (229,230) studied the influence of different temperatures and humidity conditions on keeping quality. In general, the amount of sprouting in stored onions was influenced little by the humidity, but increased with an increase in the temperature. The amount of decay appeared to show only a general slight tendency to

increase as both temperatures and humidities increased, but this was not marked. Most of the decay was identified as neck rot. For keeping both onions and onion sets in a sound dormant state the best storage conditions were found to be  $32^{\circ}$  F. and a low relative humidity of about 64 percent.

Karmarkar and Joshi (104) conducted storage experiments on the Red variety cultivated in the Bombay Province in India. Results indicated that onions sprouted more quickly (after one month) at storage temperatures from  $48^{\circ}$  to  $60^{\circ}$  F. than at higher or lower temperatures. At  $32^{\circ}$  F., onions remained dormant in storage for 6 months, while at the high storage temperature of  $90-95^{\circ}$  F. they did not sprout at all. It was also observed that sprouting was not in any way connected with root formation, as many bulbs sprouted without the appearance of new roots.

These investigators mentioned that the size of bulbs appeared to influence the rate of sprouting as, in storage at  $52^{\circ}$  F., large bulbs sprouted at a faster rate (after 4 weeks) than small ones. Changes in the amount of water, total nitrogen, reducing, non-reducing and total sugars in onions during sprouting were determined. There were no marked changes in the chemical composition of the bulb, except that there was an increase in the percentage of total nitrogen and that the percentage of reducing sugars rose slightly.

Platenius et al. (151) stated that in the experimental storage rooms at Cornell, onions have kept in perfect condition at  $30^{\circ}$  and  $32^{\circ}$  F. for six months. They would not freeze in a temperature of

30° F. At 31 - 32° F. the relative humidity apparently was of little importance; but at temperatures higher than 32°, low relative humidity was essential.

Cleaver (37) stated that storage losses depended upon the quality of the onions stored. Losses in U.S. No. 1 grade onions were 40% less than for onions from the same lots that just failed to meet the grade requirements. He recommended that onion storage should be kept as cold as possible without freezing the onions and as dry as possible without raising the temperature (near 32° F.). Low temperature was more important than low relative humidity, especially when some varieties like Southport Yellow Globe onions were stored. When Southport White Globe and Sweet Spanish onions were stored, low relative humidity was relatively more important, but not as important as low temperature.

Williams (224) in Australia proved that onions could be kept in good condition in cold storage for several months. Several packages of onions of the two varieties, Brown Spanish and Silver Skin, were placed in cold storage at various temperatures ranging from 25° to 35° F. and the best results were obtained from a temperature of 32° F. with a relative humidity of 87%.

Heiss (75) conducted investigations on the gas-storage of onions and the results indicated the very definite superiority of nitrogen gas storage over ordinary cold storage.

Recently, Rose et al. (169) advocated that a comparatively low relative humidity (70 to 75%) was very desirable for the successful storage of onions. At higher humidities onions were disposed to root

growth and decay. The commonest form of the latter was gray mold rot. The fungus inciting it could develop to some extent even at 32° F. A uniform temperature of 32° F. was found to be sufficiently low to keep onions dormant and reasonably free from decay, provided they were in good sound condition and well-cured when stored.

Influence of moisture content:

Dry-weight determinations, reported by Jones and Bisson (89), were run on 24 varieties, but only 18 were grown both seasons in 1933 and 1934. Varieties that were considered mild and of rather poor storage quality, i.e. Sweet Spanish, had the highest moisture content (about 95%), whereas those that were the most pungent and kept best in storage, i.e. Red Creole, had the lowest moisture content (about 84%).

In 1949, Peterson and Foskett (147) reported on the relationship between dry-matter and keeping quality, using 60 hybrids and varieties. In general, the mild onions having a low percentage of dry matter showed the greatest tendency to top sprout, while those having high dry-matter content were the best keepers. There were enough exceptions to this general rule to indicate a possibility for selecting high-yielding mild onions with good storage quality.

The extensive experiments carried out by Woodman and Barnell (227) in England are interesting. Data indicated that a low initial water loss following harvest and a consistently low total water loss subsequently were characteristic of keepers. Onions characterized by a high initial water loss following harvest and by high total loss subsequently were definitely non-keepers.



The rate of water loss was so rapid for non-keepers in the few days following harvest that practically immediate classification into keepers and non-keepers of 'unknown' onions, for example new types, could be obtained without actual storage experiments. Water loss was demonstrated to occur from the inner and not the outer surfaces of the scales, and therefore must take place to a large extent through the neck of an onion.

In brief, a simple test carried out over a period of 2 days--the loss in weight from harvest in the two succeeding days of a group of onions weighed in the mass--should normally be sufficient to place an onion of unknown keeping quality, such as a new variety, as a keeper or non-keeper, especially if an onion of known keeping quality was included in control test (227).

#### Influence of diseases:

Tyler (207) visited 11 common storage houses and 7 cold storage houses in New York State. Temperatures in common storage houses ranged from 32.5° F. to 42° F. and the relative humidity ranged from 82 to 91%. In cold storage plants temperatures ranged from 31.5° F. to 34° F. and relative humidity ranged from 81 to 90%. Data indicated that cold storage permitted much less bulb rot than did common storage. Counts showed that the percentage of bulbs affected in the different cold storages ranged from 0.1 to 1.5, while in common storage the range was from 0.3 to as much as 25%.

The species of organisms causing rots in cold storage onions were the same as those rotting bulbs in common storage and this indicated that they were brought from the field at harvest time. Obvious-

ly cold storage temperatures were instrumental in suppressing the activities of bulb rot pathogens during the storage period.

The organisms involved in the rots of stored bulbs were Erwinia carotovora (bacterial soft rot), Aspergillus niger (black mold rot), Fusarium spp. (bulb basal rot), Botrytis spp. (neck rot), Colletotrichum circinans (smudge), and Penicillium sp. (blue mold).

Yeasts were frequently found to be associated with the bacterial soft rot. Urocystis cepulae (amut) was found in most lots of stored bulbs but appeared unimportant as a storage pathogen. The organisms most destructive to the bulbs were Botrytis spp., Fusarium spp., and Erwinia carotovora. Colletotrichum did not appear to cause any bulb decay (207).

Hedgett (22) observed the following diseases during a survey of onion storage and processing plants:

Neck rots (Botrytis allii, B. byssoidea, B. squamosa), basal bulb rot (Fusarium moniliforme), Penicillium rot (Penicillium sp.), black mold (Aspergillus niger), soft rot (Erwinia carotovora), and soft-puffy rot (Pseudomonas alliicola).

Lents (114) isolated nine genera of molds from diseased onions obtained from Indianapolis markets in 1940. These genera were Rhizopus, Penicillium, Aspergillus, Synsporium, Alternaria, Fusarium, Verticillium, Gladosporium, and Botryosporium.

In 1949, Miller (127) reported on a similar study. He mentioned that onion and tomato were hosts to most kinds of fungi identified. Pathogens occurring on onions were Aspergillus, Macrosporium, Spinelus, Rhizopus, Penicillium, Fusarium, and Sporodinia.

In conclusion, loss of marketability (storage quality) was caused by rotting, sprouting, excessive root growth, and softening or shriveling accompanied by loss of the outer dry scales. Rotting was usually the result of infection during the growth or curing of the bulbs, but infection might also follow unfavorable storage conditions (121).

## INHERITANCE OF MALE STERILITY IN AMERICAN-EGYPTIAN HYBRIDS

### Materials and Experimental Methods

This study is a part of a special cooperative project between Dr. Jones (U.S.D.A.) and the Egyptian Ministry of Agriculture. Seeds of the Egyptian variety of onion named Giza 6 were sent to Beltsville, and through the efforts of Dr. Jones a program was started to detect or induce male sterility in that variety. Crosses were made between Giza 6 and male-sterile strains of some of the American onion varieties in May, 1949. Further crossing and selfing were also made in the spring of 1950 at Beltsville.

Three crosses were originally made which involved three different plants of Giza 6, two different male-sterile Excel-986, and one male-sterile Creole plant. These crosses are referred to as lots I, II, and III in Table XXXIII.

Further crossing and selfing consisted of:

1. Selfing fertile  $F_1$  plants from the cross I (Lot IV)
2. Sibbing  $F_1$  plants (a male-sterile x a male-fertile) from the cross I (Lot V)
3. Selfing fertile  $F_1$  plants from the cross II (Lot VIII)
4. Crossing sterile  $F_1$  plants from the cross I with fertile  $F_1$  plants from the cross II (Lots VI and VII)

A part of the hybrid seed was planted by Dr. Jones in the greenhouse at the Bureau of Plant Industry Station at Beltsville, Md. The other part of the hybrid seed was planted at Baton Rouge, La. Some of the material grown at Beltsville produced scapes in the first growing season, while first-year bolting was rare in material grown at Baton Rouge.

The classification of plants in lots I, II, and III was made in the spring of 1950. Plants of other lots were classified in the spring of 1951 and 1952 in the two locations. As soon as a plant started flowering it was bagged. The male-sterile appearance of the anthers of the inflorescence was an indication of male-sterility of the particular plant so found. A hand lens (20x magnification) was used in some cases to observe dehiscent pollen grains, if any. In a few other cases aceto-carminic smears of anthers from flowers were made and examined microscopically. The presence of stainable pollen grains indicated the male fertility of the plant.

Plate XX shows a flower from a male-sterile inflorescence. Plate XXI shows a male-fertile flower at the same stage of development. In general, the anthers of male-fertile flowers are plump (stout), turgid, not light-transparent, and dehiscent pollen grains. On the other hand, the anthers of male-sterile flowers are not plump (thin), light-transparent, of pale color, and later they shrivel without dehiscing any pollen. Classification of plant inflorescences was checked at least twice, and especially during the time when the inflorescence was in full bloom. Examination was made during mid-day (about noon).

The chi-square test was used for determining goodness of fit of observed data to conventional Mendelian ratios.

### Experimental Results

Data are presented in Table XXXIII. When two different plants of Giza 6 (viz. 669 and 676) were crossed with male-sterile Excel plants, two types of breeding behavior were observed in the  $F_1$ . The progeny of the cross that involved plant 669 produced both male-sterile and male-fertile plants in a ratio of 1 to 1, whereas the progeny of the cross that involved plant 676 was entirely male fertile. Plant 671 of Giza 6 behaved in a similar manner as plant 676. On crossing 671 with male-sterile Oreole all the progeny were fertile.

When a male-fertile  $F_1$  plant from the cross ms 986 x 669 was selfed, segregation in  $F_2$  gave a good fit to a ratio of 3 male-fertile to 1 male-sterile.

The progeny of sibling  $F_1$  plants (crossing a male-sterile  $F_1$  with a sister male-fertile) segregated for a ratio of 1 male-fertile to 1 male-sterile.

From crossing male-sterile  $F_1$  plants with male-fertile  $F_1$  plants from different crosses, a 1:1 segregation was obtained.

All P values were between .30 and .90.

In spite of the fact that backcrosses were not made, these results are not explainable unless the theory put forward by Jones and Clarke (90) is applied. This theory is discussed in detail later. A portion of Table XXXIII illustrates how the genotypes of parents will need to be expressed in order to explain the ratios obtained.

Any male-sterile plant should possess the plasmagene S - determinant of the sterile cytoplasm, together with the chromogene ms in a heterozygous condition. That is, the genotype of the male-sterile plant is  $S\ ms\ ms$ . Any other genotype should be phenotypically male-fertile. However, there is a considerable sterility in Giza 6, and other types of sterility may be involved.

The conclusion reached is that Giza 6 carries the male-sterile gene ms in a heterozygous condition as well as in the homozygous dominant condition. It is suggested that male-sterile lines of Giza 6 could be easily established and perpetuated. It would be necessary at first to self heterozygous plants of the genotype  $N\ Ms\ ms$  to obtain genotype  $N\ ms\ ms$ . Then the male-sterile Giza 6 line ( $S\ ms\ ms$ ) obtained as a result of this investigation would be perpetuated through the seed by a simple series of backcrossing to the male-fertile line of the genotype  $N\ ms\ ms$ . Backcrossing continues as long as the particular male-sterile line is to be perpetuated. After a few backcrossings the male-sterile line should be practically identical with the male-fertile except for the sterility factor of the cytoplasm.



Table XXXIII. INHERITANCE OF MALE STERILITY IN CROSSES BETWEEN MALE-STERILE AMERICAN LINES AND A MALE-FERTILE EGYPTIAN VARIETY

Lot	Parents	Pedigree	Parental genotypes	Plants		Ratio F.:M.S.	P
				F.	M.S.		
				Number			
I	784 x 669	ms 986 (Excel) x Giza 6	S ms ms x H Ms ms	4	3	1:1	.70-.80
II	785 x 676	ms 986 (Excel) x Giza 6	S ms ms x H Ms Ms	4	0	1:0	
III	660 x 671	ms Creole x Giza 6	S ms ms x H Ms Ms	9	0	1:0	
IV	F. F <sub>1</sub> ; selfed 1204	ms 986 x Giza 6 . F <sub>2</sub> 784 669	S Ms ms selfed	29	8	3:1	.50-.70
V	1201 x 1204 M.S. F <sub>1</sub> F. F <sub>1</sub>	(ms 986 x Giza 6) x (ms 986 x Giza 6) 784 669 784 669	S ms ms x S Ms ms	20	15	1:1	.30-.50
VI	1202 x 1210 M.S. F <sub>1</sub> F. F <sub>1</sub>	(ms 986 x Giza 6) x (ms 986 x Giza 6) 784 669 785 676	S ms ms x S Ms ms	28	26	1:1	.70-.80
VII	1203 x 1211 M.S. F <sub>1</sub> F. F <sub>1</sub>	(ms 986 x Giza 6) x (ms 986 x Giza 6) 784 669 785 676	S ms ms x S Ms ms	16	11	1:1	.30-.50
VIII	F. F <sub>1</sub> ; selfed 1212	ms 986 x Giza 6 . F <sub>2</sub> 784 676	S Ms ms selfed	26	8	3:1	.80-.90

F = male-fertile plant.

M.S. = male-sterile plant.

### Discussion and Literature Review

The history of the development of American-Egyptian hybrids of onions began after the return of Dr. H. A. Jones, Head Horticulturist of the U.S.D.A., from his visit to Egypt early in 1949. He was invited to pay a visit to that country as a guest of the Ministry of Agriculture. He discussed all phases of onion industry in recommendations (55) submitted to the Egyptian Government for improving Egypt's important onion industry in furtherance of the U.S.D.A.'s policy of cooperating with the governments of other countries in the exchange of technical agricultural knowledge and plant material.

Onions are one of Egypt's largest export crops and are marketed as far north as Scandinavia and as far west as Central America (7). The onion variety Giza 6, now being grown to a large extent in Egypt, has keeping quality and ability to withstand rough handling as its chief attributes. Dr. Jones wrote (55):

"The production of  $F_1$  hybrids should be the ultimate objective because by their use the greatest uniformity and highest yields can be obtained. .... It will be necessary to start with male-sterile foundation stocks that have been developed by the United States Department of Agriculture. .... To make doubly sure that there will be no delay in getting the hybrid work started in Egypt, crosses have been made in the greenhouses at Beltsville, Md., U.S.D.A., between Giza 6 and male-sterile plants of two short-day varieties, Excel and Creole."

Male sterility in the onion was first reported by Jones and Emsweller (96). In 1925, a plant (pedigree 13-53) was found in the breeding plots at Davis, California, in the variety Italian Red. It cannot pollinate itself and thus cannot be carried along by seed, but

fortunately, it usually produces large quantities of bulbs, and these are used to preserve and increase this line. Its designation, 13-53, should not be forgotten, for it is probably destined to be the most important onion bulb selection ever made. Besides its contribution to hybrid onions, it has also given us the best source of resistance to downy mildew (91,96).

Since its discovery, 13-53 has been grown under a wide range of climatic conditions. During this time, seed had never been produced when the flower heads were properly protected from pollen by bagging or by isolation, but only bulbils were secured. When the flowers were well pollinated, however, they gave a heavy set of seed. Even when loaded with seed, the flower heads continued to produce bulbils (91). This indicated that self sterility was not due to the failure of the female gamete to function. The causes of sterility in this selection were investigated by Monosmith (128), who found meiosis in the pollen mother cells to be regular and the number of chromosomes to be 16, which is characteristic for this species (Allium Cepa). She stated that the first indication of abnormality was the occurrence of hypertrophy in a few of the centrally located tapetal cells. These degenerated abnormally and following this many or all of the microspores in a locule died. At the time of dehiscence the contents of a pollen sac were cemented together and remained within the anther. The same conclusions were recently reported by Barham and Munger (10).

In 1943, Jones and Clarke (90) described the mode of inheritance of male sterility in onion. They found that the male sterility condition resulted from the interaction of a recessive nuclear gene

with a non-nuclear or cytoplasmic factor. On this hypothesis it was assumed that there were two types of cytoplasm. All plants with normal cytoplasm (designated for convenience as N) produced viable pollen. All male-sterile plants possessed the sterile type of cytoplasm (S). A gene for male sterile (*ms*) also influenced pollen development when carried by plants with S cytoplasm but had no effect when carried by plants with N cytoplasm. Consequently, the 13-53 male-sterile plants belonged to the genotype S *ms ms*. Plants with N cytoplasm were male-fertile always and might belong to the genotypes N *Ms Ms*, N *Ms ms*, or N *ms ms*, since the *ms* gene had no effect in the N cytoplasm. Plants with the genetic constitution S *Ms Ms* and S *Ms ms* will also be male-fertile, in spite of the S cytoplasm, because they carry the dominant gene *Ms*.

The non-nuclear or cytoplasmic factor was inherited through the egg (maternal transmission) and not through the male parent, presumably owing to the very small amount of cytoplasm present in the male gamete.

Data, presented by Jones and Clarke (90), were obtained from  $F_1$ ,  $F_2$ ,  $F_3$ , first and second generation backcross populations of crosses made between the male-sterile 13-53 and a large number of commercial varieties.

When male-sterile plants of the line 13-53 were crossed with various male-fertile plants, three types of breeding behavior were observed in the  $F_1$ , some progenies being entirely male-fertile, others entirely male-sterile, whereas still others produced both male-sterile and male-fertile plants in a 1:1 ratio. The genetical explanation, offered by Jones and Clarke, was as follows:

From the cross  $S\ ms\ ms \times N\ Ms\ Ms$  all  $F_1$  plants will be  $S\ Ms\ ms$  and, in spite of the  $S$  cytoplasm, are male-fertile because they carry the gene  $Ms$ . The cross  $S\ ms\ ms \times N\ Ms\ ms$  gives 1 male-sterile : 1 male-fertile.

When a male-fertile  $F_1$  plant ( $S\ Ms\ ms$ ) was selfed, the  $F_2$  approximated the ratio 3 male-fertile : 1 male-sterile.

When an  $F_1$  male-fertile plant,  $S\ Ms\ ms$ , was used as the female parent and backcrossed to  $N\ ms\ ms$  a ratio of 1 male-fertile to 1 male-sterile was obtained. But in the reciprocal backcross  $N\ ms\ ms \times S\ Ms\ ms$  all of the progeny were male-fertile, since all carried  $N$  cytoplasm. The unlike behavior of these reciprocal backcrosses was additional evidence in support of the validity of this hypothesis.

Second backcrosses of the type  $S\ ms\ ms \times N\ Ms\ ms$  gave a 1:1 segregation. Second backcrosses of the type  $S\ ms\ ms \times N\ ms\ ms$  gave all male steriles. This confirmed the expectation that 100 percent male-sterile progenies could be obtained in repeated backcrosses to a stock with the genetic constitution  $N\ ms\ ms$ . This was of great practical importance in developing a breeding program (90).

In 1943, for their study of male sterility in onions, Jones and Clarke received the Vaughan Research award offered by the American Society for Horticultural Science. In 1944, Dr. Jones was awarded the William Herbert medal by the American Plant Life Society in recognition of his important contribution to onion breeding (91).

In 1950, Barham and Munger (10) reported on the stability of male sterility in onions. Italian Red 13-53 and several male-sterile lines derived from crosses of Italian Red 13-53 with Ebenezer, Early

Yellow Globe and Brigham Yellow Globe varieties followed by at least four backcrosses to the male-fertile inbred lines, were included in these studies. There was no apparent difference in pollen development under long (14.5 - 17 hours) and normal (9.2 - 14.5 hours) photoperiod. The temperature to which flower buds were exposed during the time from the formation of tetrads until the first post-meiotic division was completed appeared to be of prime importance in determining whether or not viable-appearing pollen would be produced by a male-sterile onion plant.

The term "viable-appearing" was applied to pollen grains which looked like those from normal, fertile onion plants in aceto-carminic smears.

Below 70° F. no viable-appearing pollen was found on male-sterile plants. At 70-80° F. male-sterile plants produced a fraction of one percent of viable-appearing pollen, and it was possible to germinate some of these pollen grains on sugar agar medium; however, no selfed seed resulted when these plants were caged with flies. Barham and Munger believed that the failure to get selfed seed on male-sterile plants was explainable by the low percentage of viable-appearing pollen, the tendency of the pollen to clump, and the usual non-dehiscence of anthers on these plants.

Their data also indicated that male-sterile plants crossed to *H ms ms* fertile plants as many as seven times produced no greater percentage of viable-appearing pollen than the original Italian Red 13-53 colonial line.

Little, Jones and Clarke (117) studied the distribution of the male-sterility gene (*ms*) among commercial varieties of onion. Out of 29 varieties tested, 25 contained both the *Ms* and the *ms* genes. In the shallot (*Allium ascalonicum*) the two alleles also occurred. These investigators concluded that the widespread occurrence of both the *Ms* and the *ms* genes throughout the varieties of *Allium Cepa* indicated that the mutation (presumably from *Ms* to *ms*) took place a long time ago, or else had taken place more than once; otherwise, the *ms* gene should be found in comparatively few varieties.

Another conclusion made by Little, Jones and Clarke (117) was that the nearly equal frequency of the two alleles further indicated that in the presence of normal cytoplasm, there must have been practically no selection for or against plants possessing the *ms* gene. A strong support to this conclusion was given by Barham and Munger (10) through cytological studies. They found that the homozygous *ms* gene had essentially no effect on the percentage of viable pollen produced by the plants possessing normal cytoplasm. The heterozygous factor pair in the presence of *S* cytoplasm exerted a significant effect on the percentage of viable-appearing pollen produced (i.e. the genotype *S Ms ms* produced a percentage of viable-appearing pollen lower than either the *N Ms Ms* or the *N ms ms* genotypes).

Recently, Peterson and Foskett (148) found 80 plants showing pollen sterility in the Scott County Globe variety of onion. This number was found during a survey, covering approximately 3,000 plants, of onion fields at Pleasant Valley, Iowa.

One of the interesting recent developments in applied genetics is the realization of the possible value of male sterility in the production of hybrid seed in vegetable crops. There are several cases in which male sterility has been discovered. However, most of the reported male sterilities are not of immediate practical significance. An ingenious method whereby a male-sterility was utilized for hybrid seed production in Allium Cepa has been reported by Jones and Clarke of the United States Department of Agriculture (179).

Foundation lines of male-sterile onions have been developed by the U.S.D.A. and these have been forwarded to the major seed companies, experiment stations, and various countries throughout the world. All of the major seed companies have definite breeding programs under way for the production of hybrid onion seed, and hybrid varieties are now being listed for sale in seed catalogs. Because of higher yields and greater uniformity, it is anticipated that within 5 to 10 years most of the onions grown in this country will be the hybrid types. All of these will have been derived from foundation stocks that are now being supplied by the United States Department of Agriculture (210).

#### Male sterility in plants:

Male sterility in plants is of usual interest since its inheritance is due to a number of different mechanisms. There are male sterilities resulting solely from genic action. Other cases of male sterility are strictly cytoplasmically determined. Still a third category of male sterility results from the interaction of specific genes and cytoplasm.



Male sterilities resulting solely from genic action are most common. In maize (Zea mays L.), twenty different male-sterility genes are listed by Emerson, Beadle and Fraser (59). All of these genes are independent recessives, each capable of bringing about either complete or a high degree of sterility in the male inflorescence.

In barley, Suneson (188) found that the male-sterile character resulted from the action of a single recessive gene.

In tomato, Rick (164) discovered 13 different ms genes in 16 male-sterile plants collected from tomato fields. Breeding results indicated that the male sterility of each mutant was determined by a single recessive gene.

In Cucurbita pepo L., male sterility was found by Shifriss (179) to be inherited as a recessive character whose expression was due to a single gene difference. Male sterility in Cucurbita maxima was found to be inherited in the same manner (174).

Three cases, other than onion, of male sterility resulting from gene-cytoplasm interaction are reviewed here. These were reported in flax (Linum usitatissimum), sugar beet (Beta vulgaris), and maize (Zea mays).

In 1921, Bateson and Gairdner (11) described a male-sterile condition in flax in which the phenotype of the  $F_2$  progeny depended upon the direction of the parental cross. When the procumbent strain was used as the female parent in crosses with tall flax, the  $F_2$  population segregated normal and male-sterile individuals in a 3:1 ratio. However, the reciprocal cross yielded only normal progeny. In 1927, Chittenden and Fellow (32,33) wrote that they believed that these re-

sults were due to an interaction between gene and cytoplasm. Plants were sterile only when they possessed the cytoplasm of the procumbent strain and were homozygous for a specific recessive gene normally found in tall flax. This interpretation was later confirmed by Gairdner (69).

In 1945, Owen (144) described a case of male sterility in sugar beet which involved gene-cytoplasm interaction. Assuming two types of cytoplasm, S for male sterility and N for normal, plants possessing the normal cytoplasm (N) were fertile, while plants with the sterile cytoplasm (S) were either fertile or sterile, depending upon their genic constitution. At least two pairs of genes influenced the degree of sterility. Plants with S cytoplasm and homozygous recessive for both genes were completely sterile while those individuals which were heterozygous for any pair were semi-sterile.

In 1950, Jones (82) reported on an inherited condition of pollen abortion in maize. He stated that it was brought about by recessive genes in the chromosomes and also by extra-nuclear factors presumably transmitted in the cytoplasm. These two kinds of inherited determiners were designated as chromogenes (genes in the chromosomes) and plasmagenes (genes in the cytoplasm). The two different types of genes when present together in the same plant seemed to be without effect on each other. Each gene had the same effect on pollen production as it had when acting alone.

In 1951, Schwartz (172) presented the analysis of a case of male sterility in maize which was conditioned by an interaction of three factors:

1. A dominant gene for male sterility,
2. A dominant suppressor of sterility associated with a gametophyte effect, and
3. A specific "sterile" cytoplasm essential for the expression of male sterility.

In contrast to the large number of cases of male sterility either gene-determined or due to gene-cytoplasm interaction, there exist rare instances of male sterility in which the inheritance is solely cytoplasmic. In 1933 Rhoades reported it in maize, and Gabelman studied it further in 1949.

The analysis, made by Rhoades (162), of a male-sterile condition in maize indicated that the egg cytoplasm played the chief role in the expression of the character. There was no transmission of the male sterility through the pollen of partially sterile plants. A replacement of the chromosomes in the male-sterile line with chromosomes known to be free from sterility-producing factors had no apparent effect on the degree of sterility. The nature of the pollen parent had no demonstrable effect upon the expression of male sterility. There was no indication of the male sterility being caused by a virus disease.

Gabelman's recent results (68) are of some interest. He partially characterized the cytoplasmic factor causing male sterility in maize. This factor is particulate—a whole unit or particle. The reproduction and distribution of this particle are quite similar to the reproduction and distribution of chromosomes. Dr. Gabelman assumed the presence of discrete cytoplasmic particles in the micro-

sperocytes which gave rise to aborted pollen grains. Since functional pollen produced by a partially fertile did not transfer the cytoplasmic factor it could be assumed to be free of the male-sterile particle. It followed that the aborted pollen grains contained one or more of these particles. The particle number must remain constant through successive cell divisions.

Addendum:

In sexual propagation, the fusion of a male and a female germ cell forms the starting point for the formation of a new organism. Usually, the same number of chromosomes is contributed by both sexes. It is generally agreed that the genes, carried in the chromosomes, are relatively stable units which are transmitted from generation to generation and are responsible for similarities between parents and offspring. It is not so clear whether extranuclear constituents of the cell also have a certain amount of stability which may be transmitted to succeeding generations. If they do, and if they are able to influence the phenotype of the offspring, a type of transmission different from that of gene transmission will result, which may be called cytoplasmic inheritance.

In the zygote, the largest amount of cytoplasm is contributed by the female germ cell. It should therefore be expected that in cases of cytoplasmic inheritance differences between reciprocal crosses would result. Usually hybrids from reciprocal crosses are equal, but sometimes differences in reciprocal hybrids are found, especially in

crosses between different species. However, not all of them can be taken as evidence for independent, relatively stable characters of the cytoplasm (29).

The recent contribution of Sonneborn (185) on the subject of cytoplasm in heredity is interesting. He mentioned that cytoplasmic inheritance occurs in at least two forms that seem to be fundamentally different. One of them is based on self-duplicating, mutable, cytoplasmic particles--the plasmagenes-- which depend on the nuclear genes for their maintenance or normal functioning, but not for their origin or for their specificity. Plasmagenes are probably never independent of the genes, but this does not support the conclusion that they occupy in the cell hierarchy a position inferior to the genes.

Genes and cytoplasm are mutually interdependent for their maintenance and normal functioning. Evolution may proceed by parallel but independent mutations of nuclear genes and plasmagenes. Far from merely interfering with normal gene action, plasmagenes control vital and constructive activities.

The other form of cytoplasmic inheritance is distinguished from the first one in several ways, chief among which is the genic control of the specific nature of the character that is cytoplasmically transmitted. However, the physical basis and mechanism remain to be discovered (185).

## CORRELATION OF CHARACTERS

Two or more characters of a plant are often correlated. This may be due to either a pleiotropic effect of a gene or genes on different parts of the plant or to linkage. A correlation between two characters may exist when (a) there is variation within each character, and (b) when the two characters vary together toward a positive or negative direction. This relationship is expressed by the correlation coefficient. The magnitude of the correlation coefficient is a measure of the degree of association between the two characters. A significant but small correlation coefficient means that the association between the two characters is poor. A correlation coefficient above 0.5 indicates a higher degree of association between the two characters, and thus it may be used in breeding and selection practices.

The onion breeder is frequently concerned with the variability and correlations of his breeding material. A variation in his material is necessary in order to include the potentialities for all the desired characters. Most of the economic characters with which he is working are quantitative and may be the result of the action of several genes. A significant correlation between two economic characters may be caused by multiple factors, some of which may influence

both characters. Such an association may frequently present a handicap to the breeder, because if a desirable character is associated with an undesirable one, selection for the one without the other is difficult.

Four characters, namely, color of the bulb, sprouting of bulb in storage, first-year bolting, and reaction of scapes to mildew infection, were studied for correlation among  $F_2$  plants. A total of 267 pairs, of three different  $F_2$  populations, were used for detecting associations between characters. Data are presented in Tables XXXIV and XXXV.

In each  $F_2$  population, there was no correlation between sprouting in storage and resistance or susceptibility to mildew.

Concerning correlations between some other characters, the results were not consistent. For example, a significant positive correlation was found between bulb color and bolting in lots 105 and 108, but the correlation coefficient value was not significant in lot 101.

In any given type of correlation, a significant value was only found when the correlation coefficient had a positive sign. However, not all positive-sign correlations were significant.

In some particular correlations (e.g. between scape infection and bulb color) different signs of  $r$  values were obtained for the different  $F_2$  populations.

It is thought that some unknown factors were responsible for such discrepancies, and consequently any true association between variables—two taken at a time—would be overshadowed. Furthermore, the significant  $r$  values found between some of the studied characters were too small to indicate any important association between the two characters.





Table XXXV. SIMPLE CORRELATIONS OF CHARACTERS AMONG  
F<sub>2</sub> POPULATIONS FROM DIFFERENT CROSSES

Characters correlated	r Values found for lots:		
	101	108	105 <sup>(a)</sup>
Scape infection and bulb color	- .069	+.393*	+.050
Scape infection and sprouting	+.004	-.048	-.138
Bulb color and sprouting	-.024	-.102	+.357*
Bulb color and bolting	+.003	+.267*	+.300*
Sprouting and bolting	+.224*	-.010	+.200*

\*Significant at .05 level.

(a) Lot 101 is an F<sub>2</sub> population from the cross:

		Calred (944) x Red Creole (945)
Lot 108	"	" (950) " (945)
Lot 105	"	Red Creole (949) x Calred (946)

## SUMMARY

The mode of inheritance of some economic characters in the onion was studied.

1. The resistance of scapes to downy mildew was inherited as a recessive character, determined by two duplicate recessive genes. No association was found between the degree of foliage infection and that of scape infection.
2. Percentage of soluble solids behaved as a quantitatively inherited character apparently controlled by four to ten pairs of genes, with partial dominance of the low-solids percentage.
3. It was confirmed that albinism is inherited as a monogenic recessive character.
4. Dark-red color of bulbs was found to be dominant over light-red color. There were two to four pairs of genes acting as modifiers for red-color intensity.
5. Both non-bolting and sprouting characters showed absence of dominance.

6. An Egyptian onion variety, named Giza 6, was found to possess the male-sterile gene ms in a heterozygous condition. The plasmagene S and the homozygous recessive chromogene ms, originally discovered in Italian Red 13-53 in California, were successfully incorporated into Giza 6.

## PLATE I

The breeding material in the seedling stage grown  
in the greenhouse at Baton Rouge, Louisiana.



PLATE I

PLATES II AND III

An illustration of the crossing technique used by  
Dr. H. A. Jones in the greenhouses of Bureau of  
Plant Industry (U.S.D.A.) at Beltsville, Maryland.

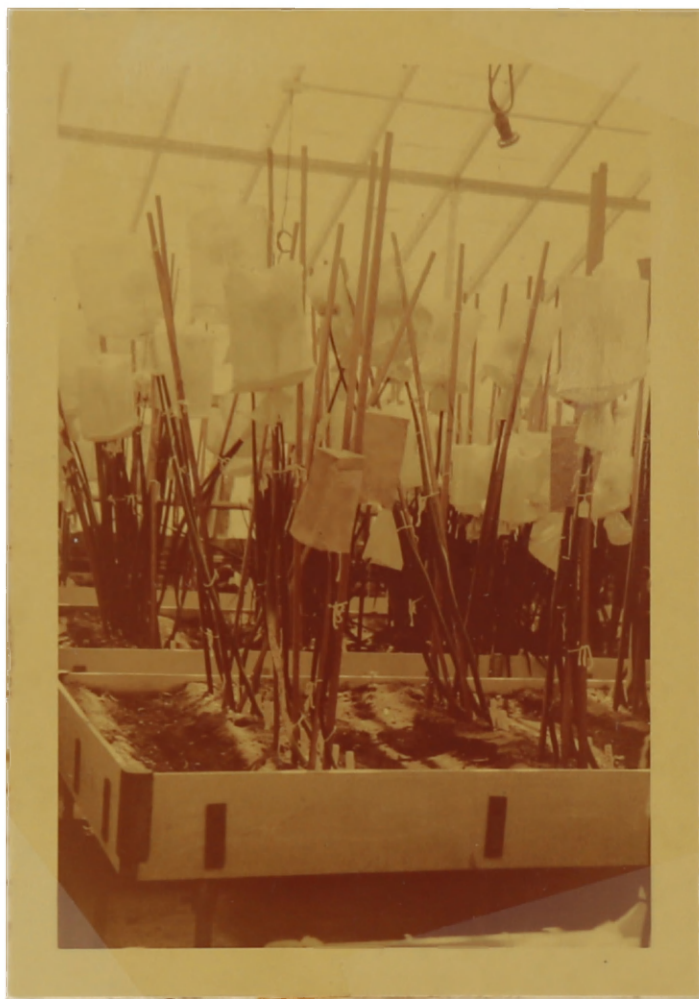


PLATE III

**PLATE IV**

**An onion field for seed production in a mildew-free area, in Idaho.**

**PLATE V**

**An onion field for seed production in Louisiana, completely destroyed by a downy mildew epiphytotic.**





PLATE IV



PLATE V

## PLATE VI

The symptoms of downy mildew (Peronospora destructor) on the leaves of Red Creole. The diagnostic feature was the presence of purplish tinge growth of the causal organism on the living onion tissues.

## PLATE VII

Lesions of downy mildew at different stages of development on the foliage of Red Creole.



PLATE VI



## PLATE VIII

Black lesions developed on the scapes of Red Creole  
as a result of infection by Peronospora destructor  
followed by Macrosporium parasiticum.



PLATE VIII

**PLATE IX**

**Albino seedlings of onions at various stages of growth. Notice the presence of two normal (green) seedlings.**



PLATE IX

## PLATE X

Seedlings of Calred-Red Creole hybrids grown at  
Baton Rouge, La. (left to right):

Light Red            (Class I)

Intermediate Red (Class II and III)

Dark Red            (Class IV)

## PLATE XI

Bulbs of Calred-Red Creole hybrids grown at  
Greeley, Colo. (left to right):

Dark Red            (1st bulb)

Intermediate Red (4 bulbs)

Light Red            (last bulb)





PLATE X



PLATE XI

## PLATE XII

Red Creole bulbs infected by Aspergillus niger.

The black spore masses that occurred between the scales tended to follow the veins.

## PLATE XIII

Bulbs of Calred-Red Creole hybrids showing dry and papery tissues resultant of infection by A. niger in common storage.



PLATE XII



PLATE XIII

## PLATE XIV

Bulbs of Calred-Red Creole hybrids infected by a  
species of *Aspergillus*.



PLATE XIV

## PLATE XV

Symptoms of blue mold disease incited by Penicillium

cyclopius:

Upper row: Natural infection of bulbs of Calred-  
Red Creole hybrids.

Lower row: Artificial infection of bulbs of Red  
Creole.

## PLATE XVI

Symptoms of blue mold, in Red Creole bulbs, induced  
by artificially inoculating the bulbs (of the lower  
row). Bulbs shown in the upper row were the non-  
inoculated check.



PLATE XV



## PLATE XVII

Bulbs of Calred-Red Creole hybrids infected by Betrytis allii. A dense layer of gray mold was developed and the old infected tissues were desiccated.

## PLATE XVIII

The appearance of sclerotia of B. allii on infected bulbs of Calred-Red Creole hybrids.



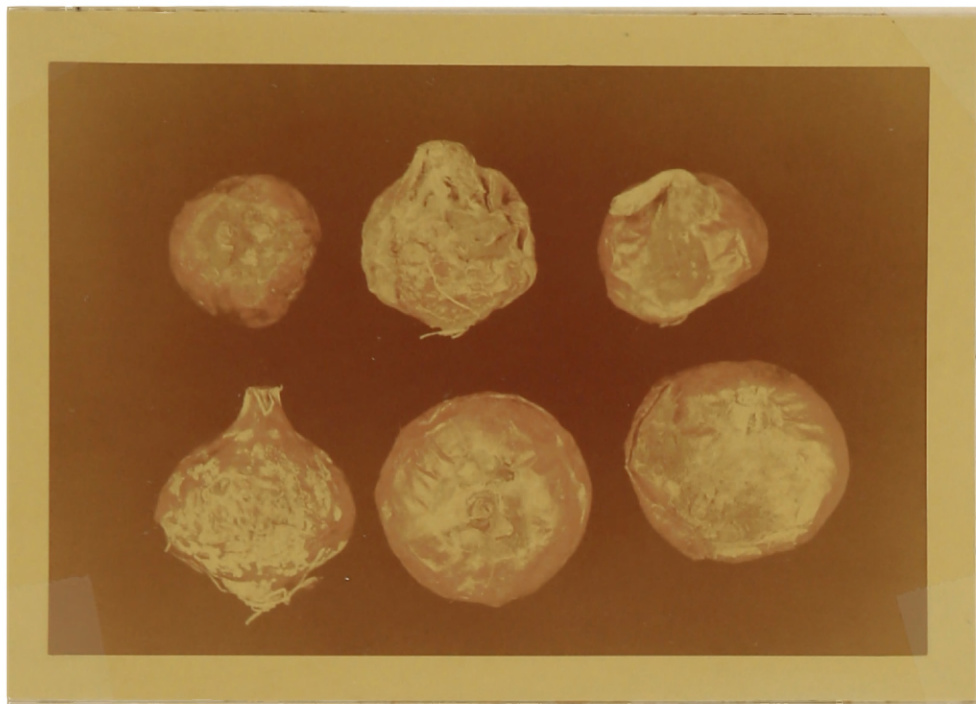
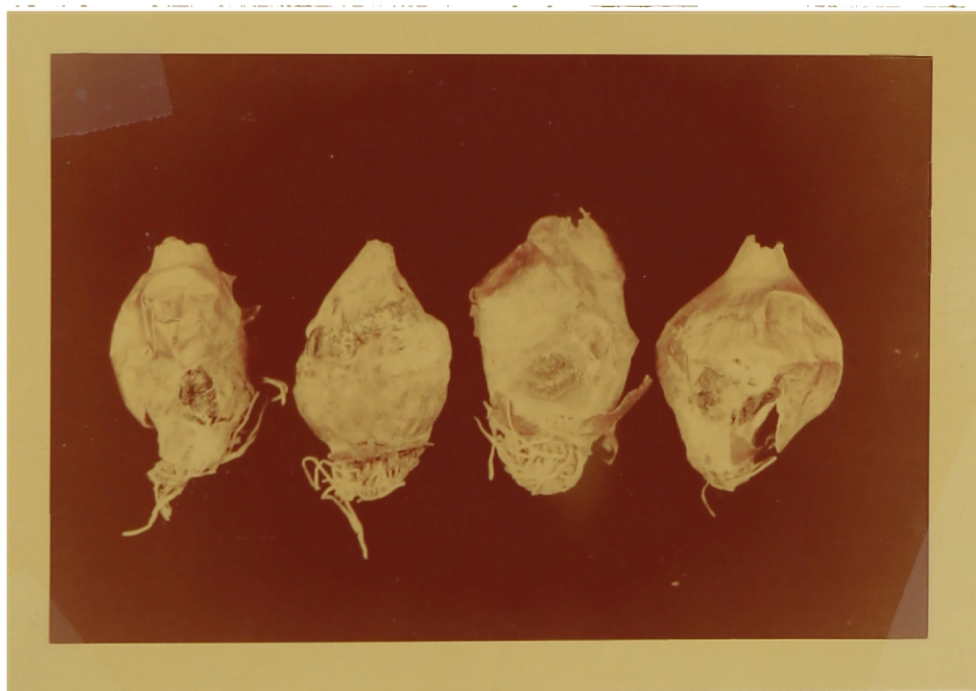


PLATE XVII



**PLATE XIX**

**Symptoms of Fusarium basal rot on Red Creole bulbs.**

**A whitish moldy growth was mostly developed at the  
base of bulb.**



PLATE XIX

**PLATE XX**

**A flower from a male-sterile inflorescence.**

**PLATE XXI**

**A flower from a male-fertile inflorescence.**

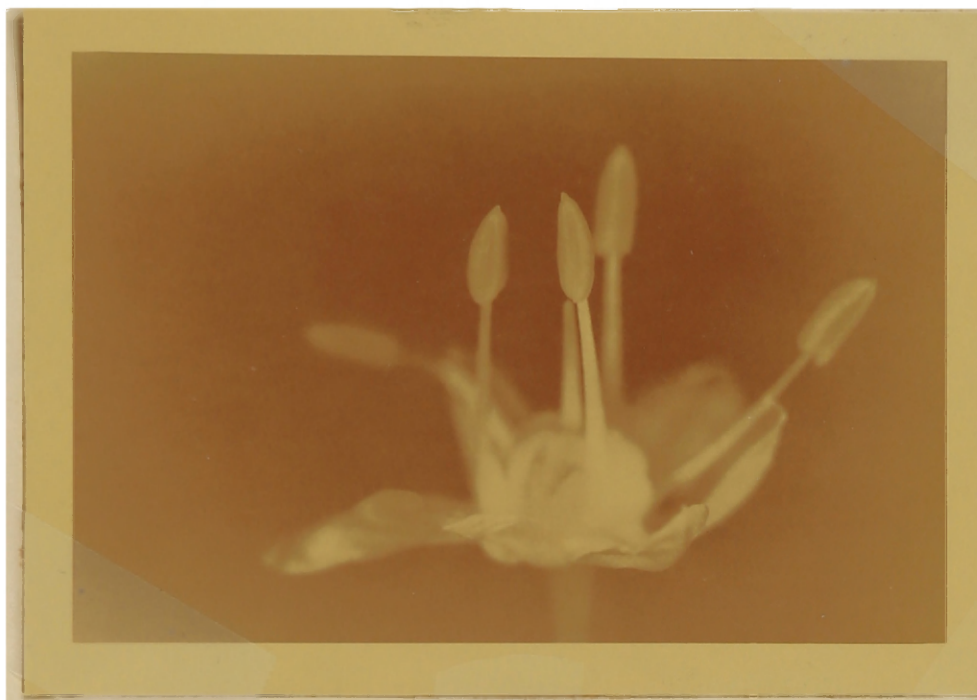
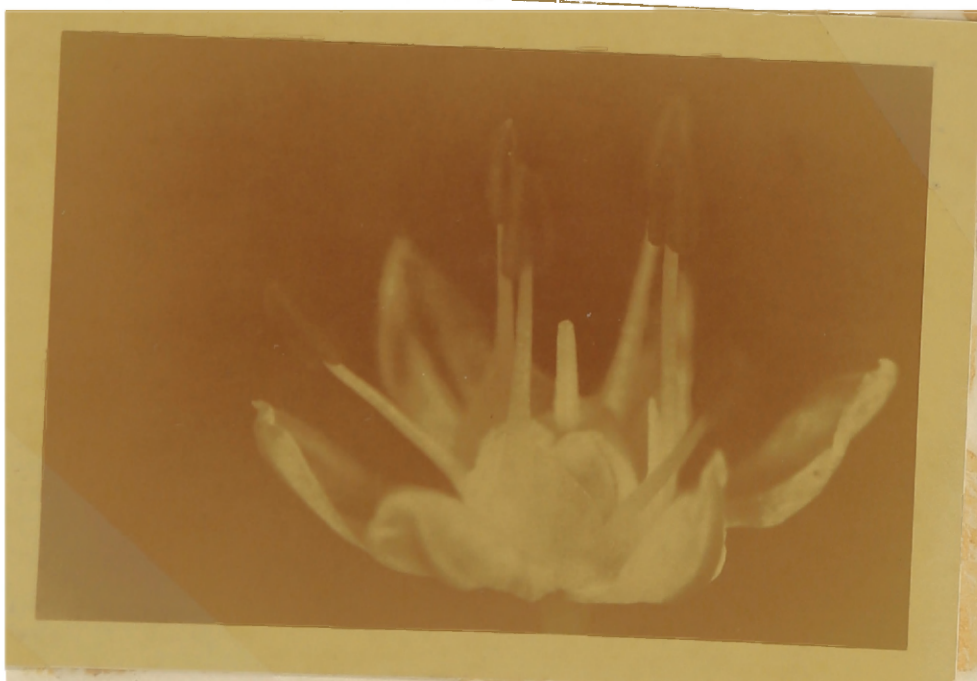


PLATE XX



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## AUTOBIOGRAPHY

Warid Abdel-Bar Warid was born January 19, 1922, at Tanta, Egypt. He was graduated from Ibrahimiah High School in June, 1939. In October, 1939, he entered Fouad 1st University, College of Agriculture, Giza, and received a Bachelor of Science degree in Agriculture in June, 1943.

In August, 1943, he was appointed by the Egyptian Ministry of Agriculture an Assistant Plant-Breeder, and occupied this position until October, 1947, when the Ministry nominated him to do post graduate work in the United States of America.

He enrolled, for a 10-month period (October, 1947 to July, 1948), at the University of Wisconsin as a graduate student doing viral-disease investigations under Dr. J. C. Walker, Professor of Plant Pathology. He continued these studies for two months at Oklahoma Agricultural and Mechanical College, under Dr. K. Starr Chester, Professor of Plant Pathology.

In October, 1948, he entered Louisiana State University. Here he received a Master of Science degree in Plant Pathology in August, 1949. He is a candidate for the degree of Doctor of Philosophy in June, 1952.

## EXAMINATION AND THESIS REPORT

Candidate: **Warid Abdel Bar Warid**

Major Field: **Botany and Plant Pathology**

Title of Thesis: **Inheritance Studies in the Onion, Allium Cepa L.**

Approved:

*E. C. Lins*

Major Professor and Chairman

*Richard Russell*

Dean of the Graduate School

### EXAMINING COMMITTEE:

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*W. H. Willie*

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Date of Examination: **April 28, 1952**

*E. C. Lins*